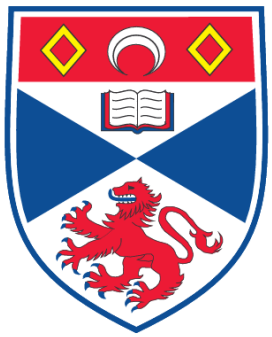
FORAGING STRATEGIES, DIET AND COMPETITION IN OLIVE BABOONS

Robert A. Barton

A Thesis Submitted for the Degree of PhD
at the
University of St. Andrews



1990

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Thesis submitted for the degree of Doctor of Philosophy,
University of St. Andrews, 1989.

DECLARATION

(a)

I, Robert Alexander Barton, hereby certify that this thesis has been composed by myself, that it is a record of my own work, and that it has not been accepted in partial or complete fulfilment of any other degree or professional qualification.

Signed [redacted] Date 8.9.89

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I was admitted to the Faculty of Science of the University of St. Andrews under Ordinance General No 12 in October 1984 and as a candidate for the degree of Ph.D. in October 1984.

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I hereby certify that the candidate has fulfilled the conditions of the Resolution and Regulations appropriate to the degree of Ph.D.

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ACKNOWLEDGEMENTS

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ABSTRACT

Savannah baboons are amongst the most intensively studied taxa of primates, but our understanding of their foraging strategies and diet selection, and the relationship of these to social processes is still rudimentary. These issues were addressed in a 12-month field study of olive baboons (*Papio anubis*) on the Laikipia plateau in Kenya.

Seasonal fluctuations in food availability were closely related to rainfall patterns, with the end of the dry season representing a significant energy bottleneck. The distribution of water and of sleeping sites were the predominant influences on home range use, but certain vegetation zones were occupied preferentially in seasons when food availability within them was high.

The influence of rainfall on monthly variation in dietary composition generally mirrored inter-population variation. Phytochemical analysis revealed that simplistic dietary taxonomies can be misleading in the evaluation of diet quality. Food preferences were correlated with nutrient and secondary compound content. The differences between males and females in daily nutrient intakes were smaller than expected on the basis of the great difference in body size; this was partly attributable to the energetic costs of reproduction, and possibly also to greater energetic costs of thermoregulation and lower digestive efficiency in females.

A strongly linear dominance hierarchy was found amongst the adult females. Dominance rank was positively correlated with food ingestion rates and daily intakes, but not with time spent feeding or with dietary quality or diversity. In a provisioned group, high-ranking females occupied central positions, while low-ranking females were more peripheral and were supplanted more frequently. In the naturally-foraging group, the intensity of competition was related to the pattern of food distribution, but not to food quality, and was greater in the dry season than in the wet season. The number of

neighbours and rates of supplanting were correlated with rank, and evidence was presented that high-rankers monopolised arboreal feeding sites.

CONTENTS

CONTENTS, cont.

CHAPTER 1: INTRODUCTION

The study of primate social behaviour has been characterised by something of a thematic schism. On the one hand, many researchers have been interested in the relationship between animals' environments and their mating systems and demography, an area of study known generally as socioecology. This was chiefly stimulated by pioneering comparative work on birds by Orians (1961) and, in particular, by Crook (1964), who later extended the approach to primates (Crook and Gartlan, 1966). On the other hand, some researchers, notably Robert Hinde and colleagues, have carried out extensive investigations into the complex nature and dynamics of social interactions and relationships (Hinde, 1969, 1976, 1979, 1983a; Hinde and Simpson, 1975; Hinde and Stevenson-Hinde, 1976; Datta, 1981), and into the relations between inter-individual processes and social structure (Seyfarth, 1977, 1978; Colvin, 1982). A little more recently, some attempts have been made to integrate these two disparate trends, in order to produce coherent models of primate social evolution (Wrangham, 1979, 1980, 1983; Dunbar, 1988; van Schaik, 1989). The aim of this thesis is both to advance the study of primate ecology, and, specifically, to continue the trend of interpreting social relationships from an ecological point of view.

The *Papio* baboons have been perhaps the most intensively studied of all primate genera (e.g. Zuckerman, 1932; DeVore and Washburn, 1963; Crook and Aldrich-Blake, 1968; Rowell, 1966; Altmann and Altmann, 1970; Smuts, 1985; Strum, 1987). To some, it might therefore seem difficult to justify further

studies; do we not know all we want to know? In fact, the advanced state of our knowledge about some aspects of baboon behaviour makes continued study all the more interesting, because it enables us increasingly to interrelate social, life-history, demographic and ecological variables. By integrating such information, it may eventually be possible to construct a socioecological model for the genus which is unique in its completeness.

The *Papio* baboons inhabit a wide range of habitats (mainly in sub-Saharan Africa, but extending north as far as Saudi Arabia in the case of *P.hamadryas*), including forest, swampy woodland, savannah, desert, and high montane slopes (DeVore and Hall, 1965; Rowell, 1966a; Kummer, 1968; Altmann and Altmann, 1970; Jouventin, 1975; Hamilton *et al.*, 1976; Stammbach, 1987; Norton *et al.*, 1987; Whiten *et al.*, 1987; Dunbar, 1988). This has contributed to their reputation as ecological generalists, a reputation consolidated by studies of their feeding behaviour, which have characterised them as omnivores with diverse and seasonally variable diets. Thus baboons are known to eat grass blades, leaves, flowers, fruit, seeds, roots, bulbs, tubers, corms, gum, bark and vertebrate and invertebrate animals, and all of these foods appear in the diets of some individual groups or populations (DeVore and Hall, 1965; Crook and Aldrich-Blake, 1968; Altmann and Altmann, 1970; Hamilton *et al.*, 1978; Post, 1978; Sharman, 1980; Norton *et al.*, 1987; Whiten *et al.*, 1987). Dunbar (1988) argues that, excluding the forest-dwelling mandrill (*Papio mandrillus*) and drill (*Papio leucophaeus*), variation in diet between populations reflects purely the constraints of

local habitats, rather than species-specific adaptations. Dunbar has shown that, while there is much dietary variance between species, this is not significantly different from the amount of variance *within* them, and he has therefore suggested that this group constitutes an ecologically flexible, but homogenous taxon. Indeed, the so-called common or savannah baboons (*P.anubis, P.cynocephalus, P.ursinus* and *P.papio*) may be best regarded as a single superspecies (Thorington and Groves, 1970).

This ecological flexibility within the *Papio* baboons is paralleled by variation in demography and social organisation. Small, one-male units are found at low population densities in high-altitude montane populations of *P.ursinus* (Whiten *et al.*, 1987), and in *P.hamadryas* inhabiting arid and semi-arid regions of Ethiopia and Saudi Arabia (Kummer, 1968, Kummer *et al.*, 1985). In Ethiopia, *P.hamadryas* one-male units are nested within larger bands, which appear to be homologous with savannah baboon groups (Dunbar, 1988). Dunbar (*op. cit.*) argues that this substructuring into one-male units is a consequence of poor food availability combined with low or moderate predation pressure. Bands coalesce at sleeping sites, probably because of a shortage of suitable refuges (Kummer, 1968). Regular migration between one-male units by females is known in *P.hamadryas*, and suspected in montane *P.ursinus* (Sigg *et al.*, 1982; Anderson, 1982; Whiten *et al.*, 1987).

Amongst woodland- and savannah-dwelling populations, by contrast, densities are generally higher, and groups rarely

break down into smaller units (an exception being *P.papio* - see Dunbar, 1988, for details), resulting in large, cohesive, multimale groups, within which females generally remain throughout their lives (Altmann and Altmann, 1970; Harding, 1973; Rasmussen, 1981; Moore, 1984; Stammbach, 1986; Dunbar, 1988 - but see also McCuskey, 1975; Hamilton and Bulger, 1987). In these groups, females have strongly differentiated, enduring networks of social relationships, characterised by grooming bonds, especially between close kin, and linear dominance hierarchies (Rowell, 1966a; Hausfater *et al.*, 1982, 1987; Collins, 1984; Smuts, 1985; Strum, 1987). The situation seems to be similar amongst montane populations of *P.ursinus* living at relatively low altitude and high population density (Seyfarth, 1976; Whiten *et al.*, 1987; Byrne *et al.*, 1989). Close relatives support one another in aggressive interactions, resulting in the phenomenon of rank "inheritance" (Seyfarth, 1976; Walters, 1980; Hausfater *et al.*, 1982; Strum, 1987), a pattern also commonly found amongst female macaques (see Gouzoules and Gouzoules, 1986, for a review). In the large multi-male groups found in woodland and savannah habitats, males form exclusive but transient consortships with sexually receptive females (Hausfater, 1975; Bercovitch, 1984; Smuts, 1985). However, there are also more lasting affiliative bonds, formed between particular males and females, which may be homologous with the one-male units found in *P.hamadryas* (Dunbar, 1988). These persist outside the period of female sexual receptivity, and extend to friendly and protective behaviour by males towards females' juvenile offspring (e.g. Smuts, 1985).

Both long-term projects and targeted field studies of *Papio* baboons have thus provided a wealth of information about the nature of social organisation, the dynamics of social relationships, demography, and, to some extent, about life history variables (see Altmann *et al.*, 1977; Altmann, 1980; Hausfater *et al.*, 1982; Nicolson, 1982; Altmann *et al.*, 1985; Bulger and Hamilton, 1987; Smuts, 1985; Strum, 1987; see Dunbar, 1988, for a synthesis). A certain amount is also known about their ecology (see DeVore and Washburn, 1963; Crook and Aldrich-Blake, 1968; Altmann and Altmann, 1970; Altmann, 1974; Hamilton *et al.*, 1978; Post, 1978; Sharman, 1980; Strum and Western, 1982; Whiten *et al.*, 1987; Dunbar, 1988). There are, however, significant gaps in our ecological knowledge. Little work has been done on the determinants of dietary selectivity (Hausfater and Bearce, 1976; Hamilton *et al.*, 1978; Whiten *et al.*, in press), and in this respect, studies of baboons, and indeed of cercopithecines generally, have somewhat lagged behind studies of colobine primates and ungulates (e.g. Field, 1976; Stanley Price, 1977; Hoppe, 1977; Hladik, 1977; McKey *et al.*, 1981; Waterman, 1984; Davies *et al.*, 1987; Hay and van Hoven, 1989). We also know virtually nothing about nutrition and energy requirements, or their seasonal and individual variation (Stacey, 1986 - see also Iwamoto, 1979, on *Theropithecus gelada*). Similarly, we have only a fairly rudimentary understanding of the availability and distribution of the relevant resources, their seasonal variation, and relationships with demography, ranging patterns, and reproductive activity.

Research in primate socioecology has been chiefly concerned with correlations between environmental features and group parameters, such as group size, gross social structure, and territoriality, and falls within Rasmussen's (1981) category of "proximate social ecology"; group-level variation in social behaviour is described and adaptive arguments are either explicitly made or implied, but are not related functionally to the interests of individuals. Thus the predominant unit of socioecological study has been the group, rather at the expense of understanding individual strategies and intragroup processes (interactions and relationships). In Rasmussen's words, "The "social" bit of social ecology has been largely left out". This matters because, in accordance with the sociobiological perspective, social structure is to be seen as the outcome of reproductive strategies pursued by individuals, rather than by groups (Maynard Smith, 1964, 1976; Wilson, 1975; Dunbar, 1988; Crook, 1989).

On this view, the building blocks of adaptive explanations for social organisation must be studies which document the consequences of *individuals'* ecological strategies for their inclusive fitness, or at least for correlates thereof, an area of investigation which Rasmussen (1981) has termed "functional social ecology".

These considerations lead to the conclusion that the functional significance of demography and social structure cannot be fully appreciated without understanding the adaptive nature of individuals' involvement in relationships, a principle which has been at the heart of theoretical work by

Richard Wrangham (1979, 1980, 1983, 1986). He argues that, because the constraints operating on reproductive success in males and females are different, it is necessary to construct adaptive arguments on the basis of their divergent strategies; for females, the critical constraint is expected to be nutrition, because this limits physiological investment in offspring, and hence reproductive rate and infant mortality (Murphy and Coates, 1966; Sadleir, 1969; Buss and Reed, 1970; Belonje and Niekerk, 1975; Dittus, 1975; Altmann *et al.*, 1977). The direct physiological costs of reproduction for males are minimal by comparison, so the chief constraint on male success is expected to be access to receptive females. The social structure of groups can then be seen as an emergent property of the interplay between male and female strategies. Thus, large, matrilocal, female-bonded groups, such as those found in savannah baboons, are thought by Wrangham (1980) to be founded on alliances formed between females for the cooperative defense of patchily distributed resources.

Wrangham's (1980) model has been criticised by some authors for its complete reliance on feeding competition between females as the explanation for the evolution of female-bonded groups (van Schaik, 1983, 1989; van Schaik and van Hoof, 1983; Dunbar, 1988). These authors argue that, while feeding competition can have a profound impact on social organisation within groups, the tendency of diurnal primates to live in groups in the first place may be best understood with reference to predation pressure. Wrangham (1983) has supported his model by pointing out that it is the only one which simultaneously explains both group-living and the

internal structure of groups. Parsimony is not always the best criterion for choosing between models, however, and there is no reason in principle why a unitary functional explanation for group-living and female-bondedness is necessarily the correct one.

Despite doubts about the adequacy of feeding competition as an explanation for group-living *per se*, there has been considerable interest in the idea that it is related to the internal *structure* of primate groups (van Schaik, 1989). In particular, aspects of relationships between females have been interpreted as the outcomes of individuals' social foraging strategies for the enhancement of reproductive performance, through the medium of nutritional status (Dittus, 1979; Post *et al.*, 1980; Wrangham and Waterman, 1981; Wrangham, 1983; Whitten, 1983; Harcourt, 1987, 1989; van Schaik, 1989). Thus, competition amongst adult females is an important focus of the present study. It is not possible to measure reproductive success in a short-term study of a long-lived species, and I concentrate on the direct nutritional implications of competition; it is then the task of longitudinal projects to establish whether the presumed link between individuals' nutritional and reproductive profiles actually exists.

Relatively few studies of primate ecology have involved attempts to estimate absolute rates of nutrient intake, mainly because of the methodological difficulties (see Chapter 6). Such estimates would be useful, both for analysing comparative nutritional trends across species, and for examining seasonal

trends and differences between individuals within groups. Feeding time budgets are appropriate where the concern is expressly with the allocation of time to different activities or areas of the home range, but, in the evaluation of nutritional variation, estimates of actual intakes are preferable. For example, where researchers have failed to find correlations between dominance and foraging success, using only feeding time budgets as measures of the latter (see Harcourt, 1987, 1989, for reviews), the possibility always exists that feeding rate or the quality of food garnered are the crucial variables mediating rank-related effects on nutrition. Similarly, the significance of seasonal variation in the amount of time spent feeding is difficult to interpret, because it will be unclear whether increases reflect greater food availability or lower feeding efficiency. This latter problem is also exacerbated by the lack of information on overall food availability, a subject tackled in Chapter 3.

In summary, the aims of this thesis are to investigate the behavioural and social ecology of a group of olive baboons (*Papio anubis*), using detailed quantification of both environmental parameters and behaviour. Analyses of group-level phenomena, such as ranging, habitat use and diet, will be complemented by examination of intragroup differences in feeding and nutrition, with particular reference to the implications of sexual dimorphism, the physiological costs of reproduction, and competition between adult females.

CHAPTER 2: STUDY SITE AND METHODS

1. GEOGRAPHY

The study site is located about 40 km north of Nanyuki on the eastern edge of the Laikipia plateau of central Kenya (see map in fig. 2.1). Much of the district is privately owned ranchland, the rest belonging to local pastoralists. The Uaso Ngiro Baboon Project is based at Chololo Ranch, owned by the Jessel family. It ranges in altitude between 5300-5600 ft. above sea-level and covers an area of 15000 acres. It is bounded to the north, south and west by other private ranches, and to the east by the Ndorobo Reserve, a tribally owned area inhabited by Samburu and Ndorobo pastoralists. However, access to these areas is not restricted by fencing, and the home range of the study troop straddled the intersection of the boundaries of Chololo Ranch, Male Ranch to the north, and the Reserve to the east.

2. GEOLOGY, TOPOGRAPHY AND VEGETATION

The main study area (i.e. approximately the home range of the study troop) encompassed the eastern edge of Chololo Ranch, the south-western section of Mbale Ranch, and the western edge of the Ndorobo Reserve (henceforth referred to simply as "the reserve") where it borders with the private ranchland. The area comprises about 50 km^2 of undulating dry woodland and wooded and bushed grassland[1], dominated by various *Acacia*

[1] In describing the habitat I follow the nomenclature established by Pratt *et al.* (1966).

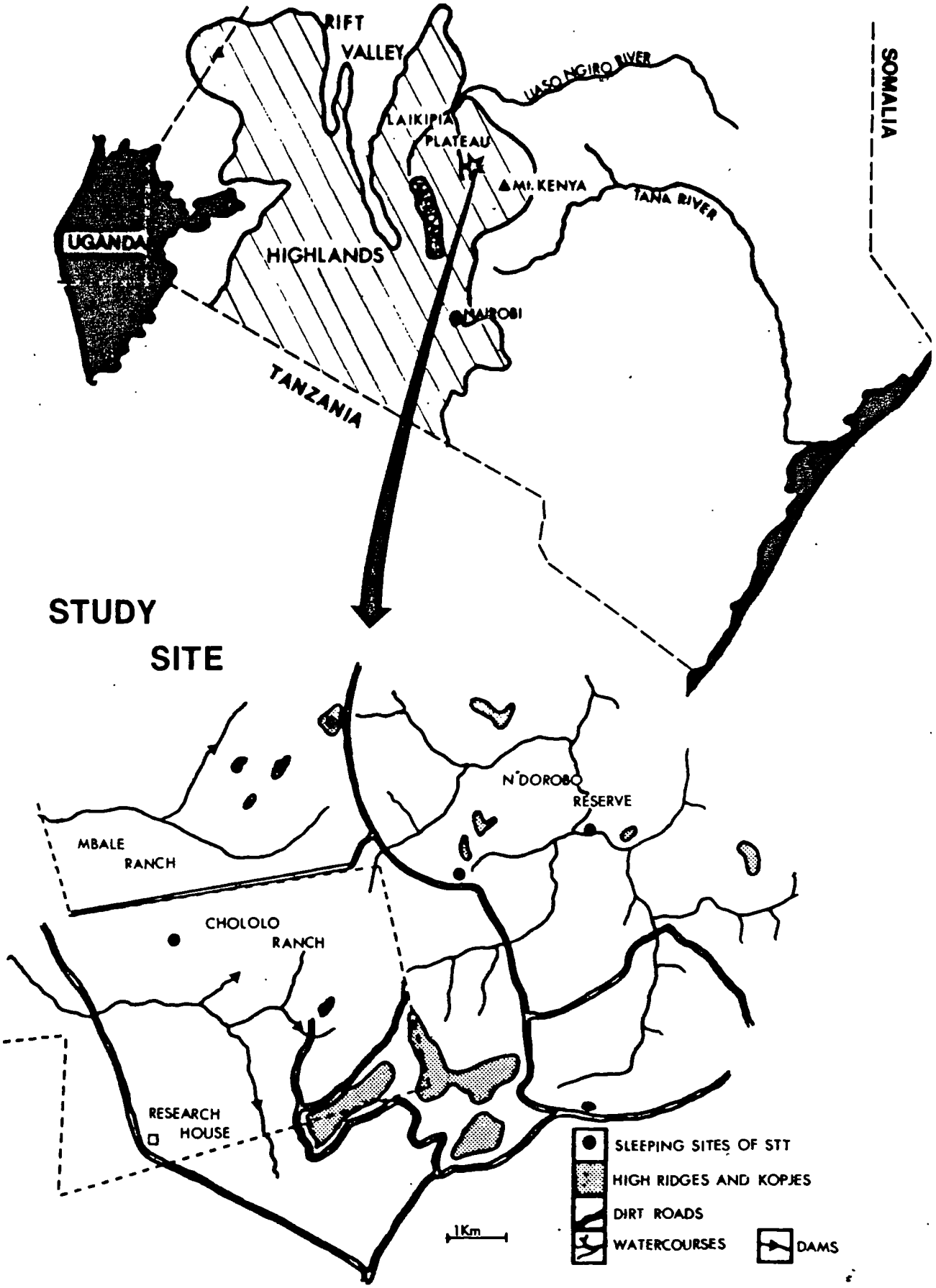


FIGURE 2.1: MAP OF THE STUDY AREA

species, and punctuated by large granitic inselbergs or "kopjes". The soils are chiefly clay loams and gravelly clay loams developed on basement complex metamorphic rocks (gneisses, migmatites and granites)[2] but there is considerable variation in the condition and fertility of the soils within the study area, due principally to local differences in slope gradients and grazing pressure. Three main geovegetational associations can be differentiated[2]:

1. The major part of Chololo Ranch itself, and Male Ranch to the north, consists of gently rolling non-dissected plains with low ridges and smooth valleys. The soils are well drained, moderately deep to deep clay loams with high natural fertility and medium to high water capacity. The vegetation almost throughout consists of *Acacia etbaica* and *Acacia mellifera* woodland and wooded grassland (with *Kyllinga/Cynodon/Tragus* understory), grading in places to open *Kyllinga* grassland. Other common *Acacias* in the area are *A.tortilis* (on well drained slopes), *A.seyal* (around gullies), *A.nilotica* and *A.brevispicata* (both widespread). Whistling thorns (*A.drepanolobium*) occur chiefly in extensive stands outside the main study area, but some small patches exist within it. Common shrubs are *Lycium europaeum*, which in places forms dense thickets, the abundant "sodom apple" *Solanum incanum*, *Grewia tembensis* and *Asparagus africanus*. The understory is dominated by short and medium height perennials, principally *Kyllinga alba*, *K.alata*, *Cynodon plectostachyus*, *C.dactylon*, *Tragus bertorianus*, *Michrochloa*

[2] Information from Kenya Soil Survey

kuntii, *Aristida kenyensis* and *Pennisetum* and *Eragrostis* species. In places where the soil has been disturbed, such as at the long-disused sites of human settlement, the corm-bearing sedge *Cyperus blysmoides* tends to dominate. Narrow strips of *Acacia etbaica* groundwater forest, with stands of *Acacacia seyal* occasionally interspersed, are associated with a system of seasonal watercourses draining westwards to the Uaso Ngiro River. In three places the watercourses have been dammed to provide a year-round source (barring extreme droughts) of water for cattle, and around the two lower-lying of these dams, more extensive patches of forest have grown up. The understory vegetation is sparser in these areas, with *Cynodon plectostachyus*, *Chloris roxburghiana* and *Penissetum mezianum* predominating. There are several kopjes in the area, used as sleeping sites by baboons. They consist of large, steep-sided blocks of exfoliating granite whose ledges and cracks support a few fig trees (*Ficus ingens*). Scattered stands of the giant spurge *Euphorbia nyikae* are localized particularly around the bases of these kopjes and in other well drained rocky places.

2. The second area comprises the south-eastern corner of Chololo, overlapping onto the western part of the Reserve. It consists of a system of high, steep ridges with massive outcrops and boulder-strewn footslopes. On its northern side it is dissected by two valleys containing vertical-sided sandy gullies up to twenty-five feet deep. The soils are excessively drained, shallow and very shallow gravelly and loamy soils on the upper slopes, becoming deeper , less

gravelly and more water-retentive as gradients flatten out lower down. Tree cover is relatively sparse, with *Acacia etbaica* and *A.mellifera* the dominant species (with *Themeda triandra/Eragrostris* spp. understory). A few clumped stands of *Euphorbia nyikae* are present. There has been considerable gullying and erosion damage on the north-eastern slopes, and here there are extensive patches of bare soil. Along the gullies there are strips of *Acacia etbaica* groundwater forest.

3. To the east of the private ranchland is the Ndorobo Reserve. The topography here is generally intermediate between the previous two areas, consisting of rolling hills and valleys with rock outcrops on ridges. The inselbergs tend to be lower and less steep than in the second area, but there are several massive rock outcrops. The main distinction is in the condition of the soils and the vegetation. The soils are well drained friable clay loams and gravelly clay loams that have been seriously affected by water erosion (partly as a result of heavy grazing pressure from pastoralists' livestock). In most places, over one half of the surface layer has been removed. In others, erosion has proceeded into the subsoil, and on some slopes the bedrock has been exposed. The vegetation is generally more arid-adapted than in the rest of the study area: *Acacia etbaica* and *Acacia mellifera* still dominate in many places, the former particularly around gullies and and on lower slopes, the latter frequently forming dense thickets; but dry *Acacia tortilis* woodland and wooded grassland and stoneland is widespread on well drained slopes. The understory is sparser, with the xerophytic plant *Sansavieria intermedia* abundant, and *Tragus bertorianus* and

Eragrostis spp. the dominant grasses. In some places the compacted gravelly soil is bare of any plants. Several patches of the introduced prickly pear cactus (*Opuntia vulgaris*) exist. A system of seasonal watercourses drains northwards, forming deep-cut gullies, along which there are a number of stands of large fever trees (*Acacia xanthophloea*). Once again, but this time in greater numbers, *Euphorbia nyikae* trees are found in clusters along the ridges and around rock outcrops.

3. CLIMATE AND SEASONALITY

Rainfall and maximum and minimum temperatures were recorded daily. The study site falls into the category of "dry savannah", which is defined as having an annual rainfall of between 300 and 900 mm. (Delany and Happold, 1979). This habitat type is prone to considerable variability in annual rainfall: total precipitation in the twelve months from October 1985 was 544 mm., whereas it was only 386 mm. in the following twelve months. During the study year (January-December 1986 inclusive) 580 mm. of rain fell.

As in many parts of East Africa, rainfall is concentrated in two wet seasons, in this case roughly March through to July, and November/December (see Fig. 2.2). Maximium daily temperatures are greatest during the dry seasons (Fig 2.3): they reached a mean of 37.2^{o}C in February of the study year, topping 40^{o}C on the hottest days. At these times insolation is intense and the evapotranspiration gradient steep. Consequently, in the absence of rejuvenating showers, the herb-layer vegetation dies back rapidly (see chapter 3). This

FIGURE 2.2: MONTHLY PRECIPITATION DURING STUDY YEAR

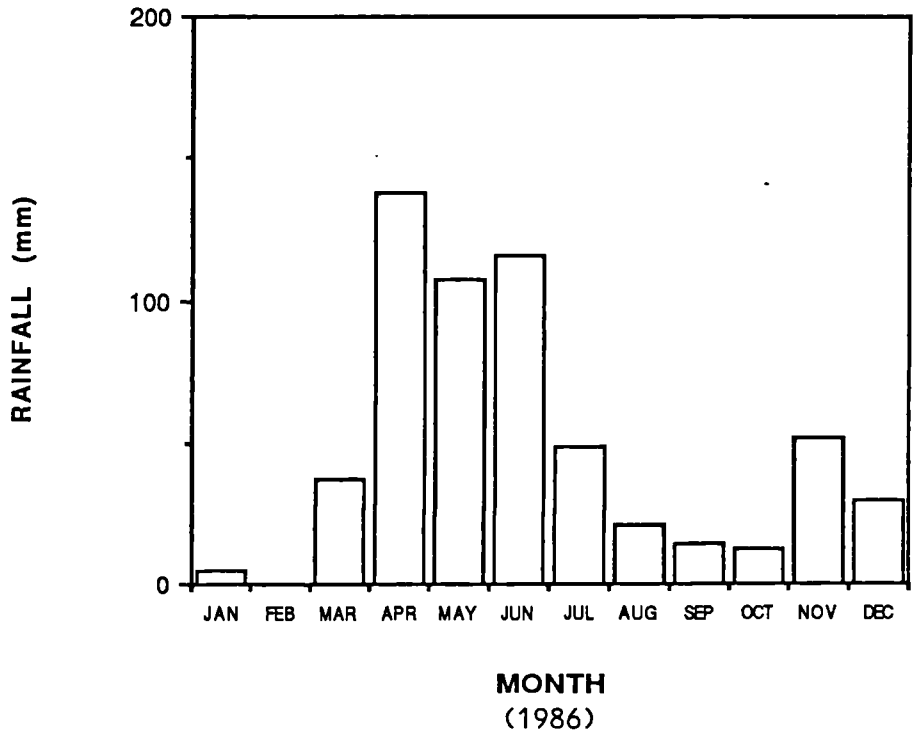
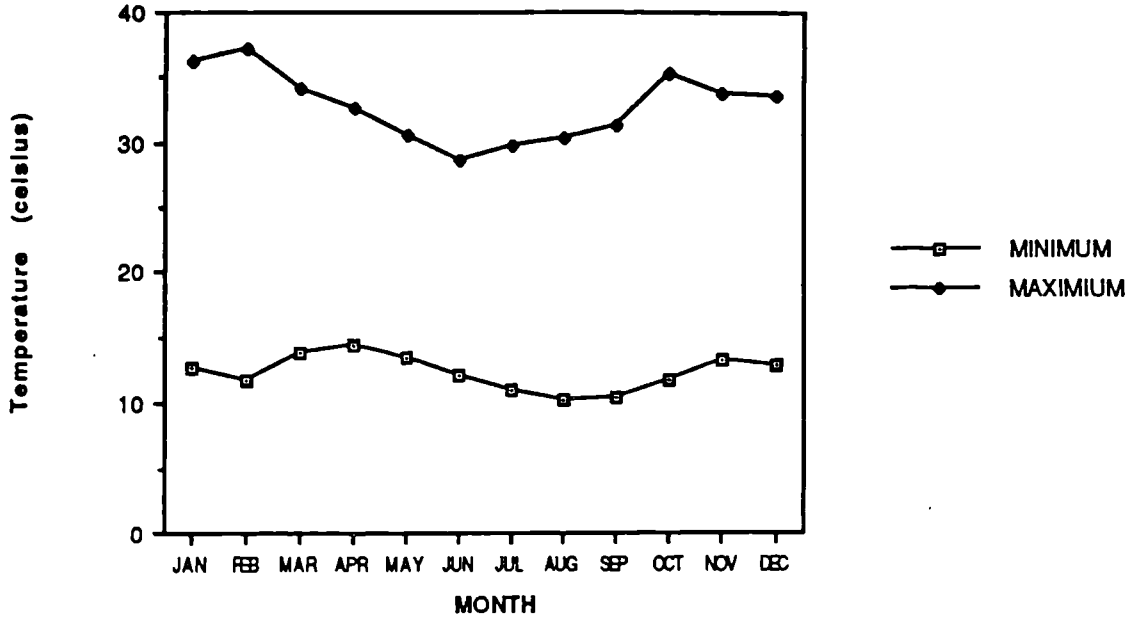


FIGURE 2.3: MEAN MINIMUM AND MAXIMUM DAILY TEMPERATURES



seasonality has great implications for baboon behavioural ecology, as the herb- layer is the source of many favoured foods.

Standing water was available in every month of the study from the four dams within the study area. During the wet season, the baboons drank from pools that accumulated in the beds of seasonal watercourses and other gullies and depressions. As the dry season progresses these pools gradually dry out, but water continues to be available beneath the sandy beds of the watercourses: the baboons both dug their own holes and exploited those made by humans.

4. FAUNA

A species list of all mammals observed in the study area is given in Appendix I. The private ranchland supports a wide range of mammals, many of which - especially the larger herbivores - seem to be effectively absent from the reserve. This is probably due to a combination of the disadvantages of greater human activity, lower plant biomass and higher density of domestic herbivore competitors. Some species were present for short periods only: elephants pass through on migration (about 200 were present for a few days in June) and wild dogs have been reported only once.

(a) Interspecific competition

Because of the great breadth of their diet (e.g. Hamilton *et al.*,1978, Post, 1978, Norton *et al.*,1987), baboons may be

susceptible to competition from a wide range of herbivores, and such competition may significantly affect their life history profiles (Strum and Western, 1982). Thus at Chololo baboons may compete for herbs and grasses with grazers such as zebra, eland and warthog, and for leaves, flowers and fruits of trees and shrubs with browsers like giraffe and gerenuk. Grazing cattle and browsing goats presumably exert similar pressure (see below). Competition from birds may even be a significant factor at certain times: von der Decken's hornbills were observed feeding on *Acacia* pods, and helmeted guineafowl used the same grass-corm sites as the baboons. Finally judging from studies of vervet monkeys in other areas of Kenya (Wrangham and Waterman, 1981, Whitten, 1983), the groups living in the east of the study troop's range presumably had extensive dietary overlap with them.

(b) Predation

All the large African felids (lion, leopard and cheetah) were seen in the study area, though they occurred at relatively low densities (lower, for instance, than at the yellow baboon study site at Mikumi, Tanzania - personal observation - but, except for leopards, higher than at Gilgil - Harding, 1973; Strum, pers. comm.). Predator alarms occured most frequently as the troop penetrated dense thickets and woodland, and involved barking, running back and climbing into trees. Hyaenas have been recorded to take baboons (Stelzner and Strier,1981), and spotted hyenas were a relatively common cause of alarms at Chololo. No actual predations on baboons were observed, though one adult female died after receiving injuries consistent with a predator attack. Local people

owned dogs, and these have been known to harass baboons at at least one other site (Harding, 1973), though no interactions were observed at this one. In principle large raptors could be a threat to juvenile animals, but the study troop never showed any reaction even to martial eagles. Likewise, the troop's lack of reaction to smaller carnivores like black-backed jackals suggested that these were not a threat.

5. LIVESTOCK AND HUMAN ACTIVITIES

Due to the poor rains at the end of 1985 and a consequent shortage of forage, all cattle were removed from Chololo Ranch by the manager, and so were not present at the start of this study. However, in June (during the long rains) 550 head of cattle were brought to the ranch and remained throughout the rest of the study period. Both goats and cows were present on Male Ranch and on the reserve, and goats in particular were commonly observed eating many of the foods exploited by baboons. The study troop avoided local people, and there was very little direct interaction: people were most frequently encountered when herding their livestock, and the baboons occasionally suffered ranging displacements of up to about 400 metres as a result. The baboons are thought to occasionally predate domestic goats, but no incidents were recorded during the study period.

No crops were being cultivated within the study area, and consequently antagonism towards baboons was minimal compared to that in many areas of Kenya (such as previously at Gilgil).

The highly habituated animals in the translocated troops (see below) occasionally caused problems by hanging around manyattas and attempting to raid food stores, but this was not the case with STT.

In summary, direct interactions between STT and humans were infrequent and the only likely significant influence of human activity on the baboons was through the impact of pastoralism on the environment, viz, soil erosion on the reserve affecting the vegetational profile, feeding competition with livestock, and the provision of permanent standing water from dams on the private ranchland.

6. BABOONS AT CHOLOLO

The Uaso Ngiro Baboon Project was established at Chololo in 1984 by Dr. Shirley Strum. Chololo was selected by Strum following extensive enquiries and survey work aimed at finding a suitable site for relocation of the Gilgil Baboon Project, situated until then near Nakuru, in the Rift Valley. Translocation to Chololo of two study troops (PHG and MLK) of olive baboons numbering 57 and 36 animals respectively was successfully undertaken in September 1984. Details of the objectives and methods of the translocation project can be found elsewhere (Strum, 1987, 1988; Strum *et al.*, 1986; Eley *et al.*, 1989). In establishing their new home ranges, both troops moved off the ranch onto the reserve, the larger troop ending up several kilometres to the east and never returning to Chololo, the smaller troop settling around Chololo's

eastern border, frequently coming back onto the ranch and sleeping at the Rough Rocks site favoured by STT. Thus, apart from during a short period of provisioning PHG and MLK on Chololo during January 1986, the home range of the study troop during the study period overlapped extensively with that of the smaller translocated troop, but not at all with that of the larger one. Both translocated troops appeared to become well integrated into the local population; dominance relations with local troops did not appear to be excessively weighted in either direction, and intertroop transfers occurred. No very obvious differences in the morphology or general behaviour patterns of the local and translocated baboons were observed.

Olive baboons observed at this study site occur in multimale troops numbering between 25 and 120 individuals (Berger (1972) found a mean troop size of 96.5 in a survey of Laikipia baboons). Following preliminary observations and survey work by Josiah Musau and assistants prior to my arrival, a large local troop known as Soitoitache (STT) was selected for habituation and study. The troop was selected because of frequent sightings and the proximity of some of its sleeping sites to the research base.

7. METHODS

(a) Following and habituating baboons

I began following STT in January 1986. The baboons were usually located at their sleeping site around 7.00 a.m. and followed on foot until 18.00-18.30 p.m., or until it was clear

where they would spend the night. Initially I recorded ranging data, made preliminary observations on feeding, and began distinguishing individuals. Censuses were attempted whenever possible, though occasions when visibilty was good enough to ensure a complete census were extremely rare (a demographic breakdown derived from knowledge of all individuals except juveniles is presented in Table 2.1). At the start, the flight distance was 40-100 metres, depending on the animal concerned (in general, adult males allowed me closer than females and juveniles), and this factor in combination with the large size of the troop and the density of the vegetation in many areas made scan sampling of activities and diet effectively impossible. However, during the next two months the flight distance decreased to 10-20 metres, and in March I considered habituation to be good enough to begin focal animal sampling (Altmann,1974).

(b) Focal animal sampling

(i) Selection of subjects and sampling strategy.

For reasons outlined in Chapter 1, I focussed chiefly on adult females, though some males were also sampled in order to provide a comparison group and to balance the analysis of overall group patterns of diet and habitat use. Females were defined as adult after the birth of their first infant, at about 5-6 years of age. Males were defined as adult when they had reached full size and developed a cape of hair on the upper back and shoulders. Definitions of all age-sex classes follow Gilgil/Uaso Ngiro project protocols, also used in Nicolson (1982) and Smuts (1985, p.21). By mid-March I could recognise most adult females, of which there were 27 (assuming

TABLE 2.1: DEMOGRAPHIC BREAKDOWN FOR STT (December 1986).

ADULT FEMALES	26
ADULT MALES	16
SUBADULT FEMALES	8
SUBADULT MALES	7
JUVENILES	29
INFANT FEMALES	4
INFANT MALES	12
TOTAL	103

no change between then and April), and several adult males, of which there were about 16. Several adult females remained very unapproachable, and these were avoided as focal subjects (subsequently there was no evidence that this significantly biased my selection on the basis of obvious characteristics like age and dominance rank). Initially eight females and three males were selected for study, this sample being gradually expanded as other individuals became more approachable. By the beginning of May I had established a final sample size of nineteen adult females and seven adult males, and it is from this date onwards that analyses of individual differences in diet and behaviour proceed; prior to that, analyses are restricted to age-sex class differences and overall group patterns. One female was later dropped from the sample due to persistently poor habituation, and replaced with another more amenable to my proximity. Details of total focal sample times for each month are given in Table 2.2.

Five time-zones were delimited for sampling purposes: 07.00-09.15, 09.15-11.30, 11.30-13.45, 13.45-1600, 16.00-18.15. Individuals were sampled for an approximately equal duration in each time-zone each month by keeping a running record of which animals had been sampled when, and selecting individuals according to which were needed to keep the tallies even. Focal samples were 30 minutes in duration, and I attempted to collect at least one of these per time-zone for every individual in each month (a total of 2.5 hours per individual per month). In this way I avoided unequal distribution of samples across time-zones and between

TABLE 2.2: MONTHLY FOCAL SAMPLE DURATIONS (TOTAL MINUTES).

Month	Adult females	N*	Adult males	N*
March	1610	9	760	3
April	950	14	370	5
May	1738	19	1162	7
June	2381	19	976	7
July	1377	19	678	7
August	1614	19	828	7
September	2468	19	1183	7
October	3216	19	1403	7
November	1556	19	702	7
December	2654	19	1159	7
TOTAL(mins)	19564		9221	-
TOTAL(hours)	326		153	-

* N=number of focal animals

individuals. A focal animal was never sampled twice on the same day, and only on successive days when a sample was particularly needed (usually towards the end of a month). The sampling strategy represents a compromise between selecting individuals at random, and selecting them according to a strict rota. The former is likely to lead to bias through oversampling of the most visible individuals, whilst the latter would have involved an unacceptable amount of time devoted to searching for animals, due to the large size of the group and the frequently dense vegetation.

(ii) Data collection and handling. All focal animal samples were collected using a Hewlett-Packard HP-71 miniature microcomputer equipped with extra memory modules to provide a total storage capacity of 32K. The HP-71 was programmed in BASIC as an event-recorder with two elements: **Continuous recording** of feeding bouts (duration, number of bites, bite-rate and food species and part), tree occupancy (bout duration, canopy size and tree species), feeding supplants (direction of supplant, identity of interactant and food type) and other social interactions (see Table 2.3 for details). Feeding bouts began when the focal animal first made contact with the food, and were terminated when the animal moved two paces without continuing to feed, or ceased orienting visually toward the food plant (after Post, 1981). **Instantaneous recording of point sample data** at 120-second intervals; activity (see Table 2.4), shade (fully in shade, half in shade, in full sunshine or sky overcast), nearest neighbour

TABLE 2.3: SOCIAL AND SEXUAL INTERACTION CATEGORIES

A. Instantaneous behaviours

Affiliative approach: approach with lipsmack, embrace etc.

Lipsmack: rapid and repeated smacking of lips, with or without vocalisation.

Threaten: hand slap, eyelid flash, vocalisation, lunge.

Attack: grab, bite, wrestle.

Avoid/grimace: physically or visually avoid, fear grimace.

Scream: fearful, high-pitched vocalisation.

Solicit aid: glance from solicitee to aggressor/ aggressee. (i) Succesful (ii) Unsuccessful.

Give aid: attack or chase aggressor/aggressee of third party.

Sociosexual: inspect, present, mount, copulate.

Feeding supplant: actor occupies feeding site (within 1 metre) following avoidance by recipient.

Other supplant: same as above, but not over feeding site.

B.Timed behaviours

Allogrooming: manual sheafing/searching through fur of other animal.

Interrupted allogrooming: bouts terminated by third-party intervention.

TABLE 2.4: ACTIVITY CATEGORIES USED IN POINT SAMPLES

FEED: in contact with food item, before ingestion.

DRINK: drink from dam or puddle.

MOVE: locomote on ground.

CLIMB: locomote in tree or on cliff.

STAND: immobile, quadrupedal stance.

REST: sit or lie.

ALLOGROOM: groom other.

AUTOGROOM: groom self.

AGGRESSION: fight, chase, threaten, scream, avoid.

OTHER SOCIAL: e.g. general affiliative.

(identity, activity and distance), number of other individuals within a ten-metre radius of focal, and habitat type (see below for details of latter). If the activity was 'feeding', then the food species and part were also recorded.

Though the data recorded in point samples were instantaneous samples of behaviour (and therefore had no duration), point samples took some time to complete and were therefore assigned a fixed duration of thirty seconds. Thus, each focal sample consisted of 1380 seconds (1 x 120 s + 14 x 90 s) of continuous sampling and 450 seconds (15 x 30 s) of point samples. Point samples interrupted recording of feeding bouts since it was not possible to keep track of feeding and record point sample data simultaneously. Feeding bouts in progress after termination of a point sample were treated as new bouts, even if they were carried over from a bout that started before the point sample. Thus, it is not possible to analyse feeding bout lengths. Tree occupancy and grooming bouts, the other behaviours for which durations were recorded, were not treated as interrupted by point samples.

Up to about 16 focal animal samples could be stored in the memory of the HP-71, and this was more than sufficient capacity for one full day's data collection (the greatest number of 30-minute samples I ever managed to collect in a day was 14). On return to the research house each evening, the data were transferred onto 130K magnetic microcassettes using a Hewlett-Packard battery-powered cassette drive. Transfer from microcassette to mainframe VAX computer in St. Andrews

following completion of fieldwork was accomplished using a Hewlett-Packard interface device. Finally, two BASIC programs (one for point samples and one for continuous samples) were written to sort the sequentially-recorded data for analysis using the SPSSX and ALICE statistical packages. Further details of programming and applications can be found in Whiten and Barton (1988)

(c) *Ad libitum* records

To supplement data on social relationships, records were kept of affiliative and aggressive interactions observed between identified individuals outside of focal animal samples. These records involved the same interaction categories as used in the latter. In addition, *ad libitum* records were kept of actual or attempted predations on or by baboons, intertroop encounters, and new foods eaten.

(d) Ranging

Using a relief map traced from a 1:250 000 scale ordnance survey map, I recorded occupancy of numbered 1/4 km^2 grid squares. Every fifteen minutes I assessed which square the main part of the troop was occupying, and recorded this on a checksheet throughout the day. The data were subsequently used in two ways. First, the length of the day journey (day range length) was estimated by calculating the sum of the vectors joining the centre of each square successively occupied. Secondly, the frequency of use of each quadrat was

summed for each month to provide information on the intensity of use of different parts of the home range.

(e) Demographic records

The following data were collected every day, or failing that, as often as possible: female sexual state and body condition (see Tables 2.5 and 2.6), consortships (identities and behaviour of consort pair, male followers, takeovers), births, deaths, emigrations and immigrations.

(f) Ecological monitoring

Three days per month were spent monitoring plant phenology and productivity by a composite of techniques, similar to those used by Byrne et *al.* (in press) in their study of mountain baboons (*Papio ursinus*). Permanent transects were established, two of 2 km and one of 1 km in length. These were located in such a way as to provide a reasonably representative sample of habitat types. Transects were oriented either north-south or east-west, and cairns were built at 200 m. intervals along them to provide a total of 28 permanent sampling points. Provisional unmarked transects were established in May, the cairns being built with the assistance of E. Anderson in June and July. Sampling techniques were as follows.

TABLE 2.5: FEMALE SEXUAL STATE CATEGORIES

A. SWOLLEN*

Numbers 1-5 represent increasing degrees of swelling of the sexual skin as the cycle progresses. Ovulation occurs in the later stages of swelling, but there is substantial individual and seasonal variation in the maximum size reached.

1: Vaginal enlargement with or without slight swelling.

2: Downward expansion of swelling to bottom of ischial callosities.

3: Backward expansion, visible from side.

4: Lateral expansion, with or without further descent.

5: More expanded version of 4.

6: Detumescent.

B. MENSTRUATING: menstrual blood visible prior to swelling.

C. PREGNANT: backdated to last day of detumescence.

D. LACTATIONAL AMENORRHEA: prior to resumption of cycles

1: Infant with natal coat colour (black).

2: Infant with transitional coat colour.

3: Infant brown.

* Gilgil/Uaso Ngiro Project protocols

TABLE 2.6: FEMALE BODY CONDITION CATEGORIES

A. NO OBSERVABLE WEIGHT LOSS

* 1: No hair loss

2: Some hair loss

3: Extensive hair loss

B. NOTICEABLY THIN

Narrowed waist, relatively high bone definition.

1 - 3: Same hair loss categories.

C. VERY THIN

Excessively narrowed waist, pelvic and other bones protrusive.

1 - 3: Same hair loss categories.

Notes: * Hair loss and weight loss were correlated, so that, for example, a score of C1 (very thin, no hair loss) is unlikely.

(i) Total herb-layer green biomass. Fluctuations in the gross biomass of green herbiage were assessed using the pin-frame method described by McNaughton (1979). Briefly, a count is made of the number of contacts between green plant material and four angled wire pins slotted down through holes in the ridge-piece of a wooden frame. In this case, the procedure was repeated eight times at each of five grassland plots by members of the UNBP, as part of their long-term ecological monitoring. Green biomass was then computed from the mean number of hits per pin using the following equation:

$$b=6.3+16.93(h) \qquad \text{(McNaughton, 1979)}$$

where b is green biomass in grams dry weight per square metre, and h is mean hits per pin. Ideally, because of differences in vegetation structure, the equation should be calibrated with clipped biomass figures from the particular study site. However, the calibration is the same for Serengeti and Amboseli, with widely divergent habitats and rainfall (D. Western, pers. comm.). Furthermore, since the main concern is with temporal variation within the site, rather than with the absolute values of the biomass figures, this is not critical.

These data, collected at approximately six-weekly intervals, have been made available to me by Dr. Strum. They provide background information on general food availability for a greater period than the more detailed quadrat data (see below). In addition, I collected pin-frame data every month, between August and December, at six plots on my transects (two per transect). These (admittedly limited) data could then be

compared directly with the quadrat data to give an idea of the efficacy of the pin-frame method in estimating an environmental parameter of relevance to baboon ecology.

(ii) Herb-layer baboon foods. The biomass of baboon foods found in the herb-layer or loose on the ground was assessed each month using 0.25 m^2 quadrats. These were placed on the ground adjacent to marker pegs one metre to either side of of the cairns, giving a total of 56 quadrats each month (equivalent to a sample area of 14 m^2). The number of items of each food type was counted within each quadrat, including non-growing items that the baboons picked up from the ground, such as dried *Acacia* flowers and seeds. Sampling was carried out at the same spots each month to avoid introducing "noise" due to spatial variation in assesssments of temporal variation. This meant that biomass could not be measured directly by removing baboon foods for weighing. Instead, items were collected for drying, weighing and phytochemical analysis from other sites. The dry weights per item thus obtained for each food type were then multiplied by the number of items counted within quadrats to give estimates of biomass. In many cases, where items comprise discrete units (such as with individual flowers, fruits and leaves) this procedure was straightforward. In the case of grass blades, however, estimates were a little cruder, because it was not considered feasible to count each individual blade. I therefore counted the number of average-sized baboon bites available, based on my observations of the animals feeding, and multiplied these figures by the dry weights of the average baboon bite. The

latter was estimated for each grass and sedge species by collecting at least one hundred "bites" in a manner as similar as possible to that observed in the baboons (these estimates were also used to calculate food intake by focal animals). Subsequently, the accuracy of the technique was checked for two grass species by counting bites available in quadrats away from the transects, predicting the biomass by multiplying the number of bites by the average dry weight per bite, and then harvesting, drying and weighing all the available blades considered edible (coarse, older blades were not generally eaten by the baboons). The predicted and actual biomass values were in close agreement for both samples (*Cynodon dactylon*, error=7.3%; *Cynodon plectostachyus*, error=4.9%). Herb-layer quadrat data are available for the eight-month period May-December.

(iii) Trees and shrubs. The biomass of baboon foods available from trees and shrubs was also assessed every month. The method involved estimating the average weight of food items per tree or shrub of a given species and size category, and multiplying this by the density of such individuals within the home range. Initially I intended to assess density using the point-centred quarter (PCQ) method developed by Cottam and Curtis (1956). At each cairn along the transects, four quadrants were delineated, defined by the intersections of bearings to the four main points of the compass. The distance to the nearest tree[3] and to the nearest shrub (at least 50 cm high) within each quadrant was measured. These were also then assigned as "focals" for phenological monitoring by marking

with string. Focal trees and shrubs were examined every month, and scored for percentage presence (0%, 1-25%, 25-50%, 50-75%, 75-100%) of leaves, flowers and fruits or pods. In the case of known or suspected baboon foods, the total numbers of items (flowers, pods etc.) were counted, or estimated when numbers were too great to count directly. These estimates were obtained in two ways. For shrubs and smaller trees, the number of items on several branches were counted, the average number per branch calculated, and this figure multiplied by the total number of branches. For trees too large to make counting of every branch feasible, the number of branches in a vertical section, two arm-spans in width, was counted and multiplied by the number of these sections in the tree.

Given the problematic nature of estimating absolute densities from PCQ data where habitats are patchy (Cottam and Curtis, 1956), and the relatively small number of PCQs in the sample, it was ultimately decided to measure densities more directly, using appropriately-sized quadrats. At each of the 28 cairns, quadrats measuring 30 x 30 m were staked out, and the number of trees and shrubs of each species and size category counted. Thus the density data were calculated from a total sampling area of 25,200 m^2. No *Euphorbia nyikae* trees appeared in any of the quadrats because their distribution is very clumped. Therefore I counted the total number of these trees within the

[3] Immature trees, defined as those not exceeding head-height, were ignored. These did not produce significant amounts of baboon foods.

home range, and calculated density by dividing by the home range size. Phenological data were not collected for this species, but the total number of edible stem segments, or "pads", was estimated in September by counting the number present on fifteen individuals. Biomass is then given by

$$b=w(n)/HRS$$

where w is the mean dry weight of pads (grams), n is the estimated number of segments within the home range, and HRS is the home range size (m^2). In using the same biomass estimate for each month I assume that availability did not vary during the study period. This is probably not wholly warranted, although there were no visually obvious changes in the condition of trees, apart from a few that became decimated by baboons, and the food was eaten in nine out of ten study months (June was the exception). The biomass estimate arrived at in September is considered to be a maximum value, since all segments that looked remotely edible were counted, despite the fact that some of these were probably not acceptable to baboons. Despite this, the biomass figure arrived at is a small proportion of the total figures for each month (1.75% and 0.49% in the months of lowest and greatest total biomass respectively), so fluctuations in availability, whatever their magnitude, could not have had an important impact on total food availability.

(iv) Sedge corms and other underground items. Assessment of underground food items is highly problematic: the obvious way is to dig up quadrats and extract , dry and weigh all food

items found. Quadrats could not be disrupted in this study because I returned to monitor the same sites each month. Partly visible semi-underground items, such as the leaf bases of sedges, were counted directly in the quadrats, though variations in their condition could not be directly assessed. The bases of *Mariscus amauropus* and *Sanseviera intermedia* were eaten in every study month and seemed to be resistant to the effects of dehydration: samples taken away from quadrats revealed that the mean wet weight of bases per plant was greater in the wet season than in the dry (*M. amauropus*: wet=0.098 grms., dry=0.076 grms., $t=3.63$, $df=5$, $P<0.05$; *S.intermedia*: wet=1.822 grms., dry=1.736 grms., $t=2.98$, $df=6$, $P<0.05$), but dry weight appears unaffected (*M.amauropus*: wet=0.033 grms., dry=0.036 grms, $t=0.34$, $P>0.05$; *S.intermedia*: wet=0.178, dry=0.190, $t=1.01$, $P>0.05$). However, not all bases are edible (baboons appear very selective about which ones they pull up, and even then may discard some) so the counts made were corrected by assessing the proportion of bases in a random sample that were edible - it is not difficult for an experienced human observer to distinguish bases which are obviously inedible from those which are at least fairly edible.

The corms of the sedge *Cyperus blysmoides*, an important food in the baboons diet in the second dry season, are entirely subterranean and could not therefore be counted in herb-layer quadrats. Instead, the density of plants was assessed from the quadrats in June (when new green growth was present). The mean number of corms per plant was estimated by counting the

number of plants in a small quadrat (0.1 m^2) away from the transects, digging this up to a depth of six inches, passing the soil through a fine wire mesh, and counting the number of corms thus extracted. Finally, corms were collected for weighing and phytochemical analysis in the dry season by D. Lochhead and S. Whiten. The biomass of corms within the home range is then estimated as:

$$b=w(dn)$$

where w is the mean dry weight of corms, d the density of plants, and n the number of corms per plant. No attempt has been made to assess variations in the availability of corms, though such variations are likely to be substantial for the following reasons. Firstly, the main sites where corms were eaten are concentrated patches of *C.blysmoides*, mostly associated with ancient sites of human settlement; these "corming sites" may become depleted with extensive use, towards the end of prolonged dry seasons. Secondly, during the rainy season, the plants presumably divert nutrients stored in the corms into the new green growth above ground. During this time it may also be physically more difficult to dig corms out, due to the relative profusion of impeding vegetation. In fact, during this study, *C.blysmoides* corms were eaten only in the dry season (August to October) and the short rains (November and December). In compiling the total baboon food biomass estimates I have therefore assumed that the corms were available in those months only. While this assumption is unlikely to be wholly realistic, including the corm estimate in the calculation of total biomass for other months does not

change the overall rank ordering of months - it simply increases the disparity between wet season and dry season (see Chapter 3). Furthermore, it is a moot point as to whether a food can validly be thought of as exerting an influence on behaviour (such as ranging) at times when it is not actually eaten. The only real problem comes in analysing determinants of what is and what is not eaten at particular times - this is not something I attempt here.

(g) Weather

Daily precipitation and minimum and maximum shade temperatures were recorded by members of the UNBP.

(h) Plant material collection and phytochemistry

Samples of plant material were collected whenever possible. In the case of baboon foods, the number of items or bites was counted as the plants were harvested. The samples were immediately sealed in plastic bags and weighed. Samples were subsequently dried to constant weight under a gas-fired grill on the minimum setting, a procedure which took a variable amount of time according to the size and nature of the material, but not less than 2-3 hours. For each sample a record was kept of the collection date, the fresh weight, the dry weight and the number of items or bites. The samples were tied up in fresh plastic bags and stored in a canvas sack

inside a dry, dark cupboard. They were checked periodically for signs of dampness or degradation.

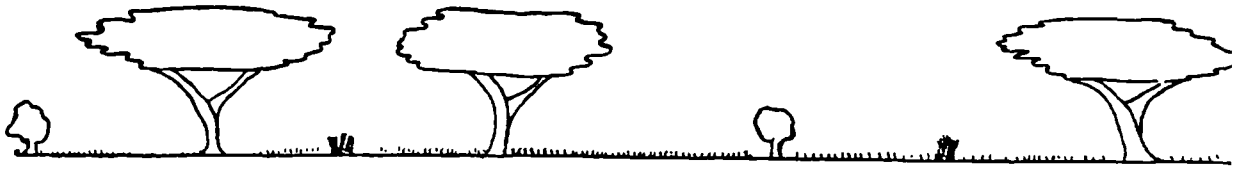
On my return to St. Andrews in February 1987, M. English carried out analyses of acid detergent fibre (ADF), total phenolics (tannic acid equivalents), and condensed tannins (quebracho tannin equivalents) on all samples, and of lipids (ether extract), and alkaloids (by reaction with Dragendorf's reagent - see Whiten *et al.*, in press) on some samples. Subsequently, the samples were also analysed for nitrogen content by the Panmure Trading Company, Monikie Granary, Dundee, using the micro-Kjeldahl method; protein content is then estimated by $N_2/6.25$ (Crampton and Harris, 1979). The results are given in Appendix III.

(i) Habitat map

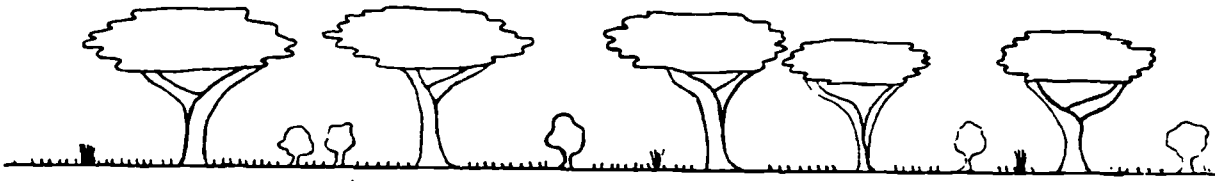
A bipartite system for classifying habitat types within the study area was established on the basis of the **density** and **species dominance** of trees and shrubs. Further distinctions were made according to whether habitats were associated with watercourses or dams, or had a sparse or relatively abundant herb-layer. Kopjes were distinguished as a habitat type in their own right since they have a distinctive vegetative make-up. No attempt was made to classify habitat types on the basis of the species composition of the herb-layer. The habitat classification system is detailed in Figure 2.4.

2. Open: grasses and herbs dominant, tree/shrub cover 0-25%.

3. Light bush: tree/shrub cover 25-50%, canopy overlap rare.
8. Light bush: with stony/rocky ground (at least 50% of surface).



4. Thick bush; tree/shrub cover 50-75%, canopy overlap frequent.
7. Thick bush: In strips along watercourses.
9. Thick bush: with stony/rocky ground.



5. Forest: tree/shrub cover 75-100%, canopy overlap extensive.
6. Forest: in strips along watercourses.

10. Kopjes and rocky ridges.

Habitat subtypes by dominant tree/shrub

a. Acacia etbaica b. A. mellifera c. A.etbaica/A.mellifera

d. A.tortilis e. A.brevispicata f. Lycium europaeum

j. A.nilotica k. Commiphora coricea/C.schimperi

m. A.xanthophloea n. A. seyal.

Figure 2.4: Habitat Classification System. Each density type is split into sub-types according to the dominant tree or shrub. Missing sub-types from the table (g,h,i,l)are those that occurred only in very small patches, beneath the resolution of the habitat map.

Having defined habitat types the scheme was used in two ways. Firstly, the habitat type occupied by the focal animal was recorded in point samples, and breakdowns of habitat occupancy in different months were then compiled. Secondly, a habitat map was produced in order to estimate the percentage of the home range covered by each of the habitat types. The two sets of results could then be put together to calculate habitat selectivity (Chapter 3). The habitat map was drawn up by tracing vegetation boundaries, viewed by walking along ridges and other high points, onto a transparency overlying the topographical map of the area. Each vegetation zone was labelled. The resulting map was subsequently analysed by D. Davies using a 3-clour plane "Pluto" graphics workstation. The procedure involved reproducing the map on a colour monitor by tracing the outline of each vegetation zone using interactive graphics procedures, and uniquely labelling each zone type with an assigned colour. A program to count the number of pixcels of each colour was then run, producing a breakdown of the relative area of each habitat type (see Chapter 3 for results).

(j) Statistical methods

Parametric tests have been used in preference to nonparametric tests wherever possible, due to their greater power (Sokal and Rolf, 1981). This has, in many cases, necessitated transforming the raw data in ways appropriate to the assumptions of particular tests. Facilities for checking assumptions within SPSSX routines were used (e.g. the "condescriptive" routine for assessment of departure from the

normal distribution, and procedures for analysis of residuals in regression). Where assumptions were not met by the raw data, I have followed Sokal and Rolf (1981), who recommend data transformations appropriate to particular problems. In general, logarithmic transformation was found to be effective in linearising relationships in correlations and regressions, and in normalising positively skewed distributions and stabilising variances correlated with means in ANOVAs. Where data were expressed as percentages or proportions, the arcsine transformation was routinely used. In t-tests, separate variance estimates were used wherever variances showed significant heterogeneity. Finally, where data were inherently ranked (e.g. as in dominance rank), or where transformation was ineffective in satisfying assumptions, nonparametric methods were used. Tests of significance are all two-tailed, unless otherwise stated.

N.B. In the continuous focal sampling of feeding, bites of foods which varied in size, such as bunches of grass blades, were differentiated according to their size (small, medium and large). Specific estimates of the dry weight per bite were then generated for each size category of each of these foods. One bite constituted one hand-to-mouth action.

CHAPTER 3: VEGETATION, FOOD AVAILABILITY AND HABITAT USE

1. INTRODUCTION

The aims in this chapter are to quantify the vegetational characteristics of the home range of the study troop, to describe the overall patterns of ranging and habitat use, and to relate seasonal variations in the food supply to ranging and habitat use.

Together with interpopulation comparisons, analysis of seasonal variation in ranging and habitat use has, to a great extent, been the stock-in-trade of primate ecologists (see for example the review by Clutton-Brock, 1977). My purpose in performing similar types of analysis here is essentially twofold. Firstly, I have the advantage of measures of absolute food availability and its seasonal variation. This is frankly rare in studies of primate ecology, a fact which has led Bishop (1984) to complain that

> " we have yet to understand the implications of "seasonality" for each species; our assumption that dry season=scarcity and wet season=abundance for all primate species needs closer examination "

It is true that, at least in baboon ecology, this assumption has been universal (e.g Crook and Gartlan, 1966; Altmann and Altmann, 1970; Post, 1978). To date there are just three published studies in which absolute food availability was estimated (Charles-Dominique and Hladik, 1971, on sportive lemurs *Lepilemur leucopus*, during one season; Watts, 1984, on mountain gorillas *Gorilla g. berengei*; and Coelho *et al.*,

1976, on howler monkeys *Alouatta villosa* and spider monkeys *Ateles geoffroyi*). There is one study on mountain chacma baboons (*Papio ursinus*) in which overall food availability was measured (Byrne, Whiten and Henzi, in press), which, indeed, laid the methodological groundwork for this study. To my knowledge, however, there have been no previous studies of savannah baboons in which plant food biomass was measured, despite the great potential value of such data in comparative work, and, excepting the three-month study by Charles-Dominique and Hladik (*op cit.*) no studies of <u>any</u> primate in which monthly variation in plant food biomass was quantified. Perhaps some of the responsibility lies with Clutton-Brock (1977), who has stated that

> " ...it is (and may always be) virtually impossible to measure variation in overall food availability. "

Having tried it, I believe Clutton-Brock's assertion to be overly pessimistic (and I thank my supervisors, Andy Whiten and Dick Byrne, for persuading me of both the possibility and the desirabilty of such measurement, while Shirley Strum introduced me to the pin-frame method of estimating total herb-layer green biomass). These measures permit a more rigorous, quantitative approach to the analysis of temporal covariation between behaviour and environment, although it should be stressed that my conclusions will of necessity be somewhat limited by the relatively short period of my study (twelve months of the six-weekly pin-frame estimates, but only eight months of actual baboon food biomasses). Analyses will be extended in future publications by incorporating data

collected using the same methods in subsequent years (by D. Lochhead and others).

Clutton-Brock (*op cit.*) warns that, even if it is feasible to measure availability of foods selected, this may be a poor estimate of overall availability if feeding becomes less selective when food is short - presumably the point is that marginal foods will not have been included in the earlier estimates, hence rendering comparisons problematic. However, this can probably be dealt with by incorporating all items which it seems likely or possible will be eaten at some stage. Of course, no monitoring system can be perfect, and, inevitably, certain foods will not be sampled adequately or at all. But so long as availability of most foods, and of all the important ones, is adequately measured, it will be valid to calculate estimates of overall biomass and to assess seasonal variation.

The second purpose of including analyses of food availability and behavioural correlates is to inform the analysis of individual differences in behaviour and foraging strategies, issues central to this study, by setting these in ecological context. There is the general point that, in trying to understand the adaptive significance of individual behaviour, it is important to know as much as possible about the ecological constraints acting on the social unit as a whole. The interpretation of sex differences in nutrition, for example (see Chapter 6), depends on our understanding of what foods are available and in what quantities. More specifically, the issues of seasonality and of social

strategies are directly related, at least with respect to one major theoretical model of the ecology of primate social structure (Wrangham, 1980) - this link will be explored in Chapter 7.

In the analyses that follow, I begin by assessing the habitat structure of the home range, and seasonal variation in food availability. I examine the influence of rainfall and address the issue of the wet season/dry season dichotomy. Subsequently I describe ranging patterns and habitat use, and relate seasonal variations in these to variations in the food supply.

2. RELATIVE ABUNDANCE OF HABITAT TYPES

The percentage of the home range covered by each habitat type, assessed by the method described in Chapter 2, is given in Table 3.1. This demonstrates the overwhelming preponderance of *Acacia* dominated woodland and wooded grassland. *A.mellifera*, *A.etbaica* and *A.tortilis* zones predominate, principally at medium densities, together making up about 81% of the home range. The habitat map in Figure 3.1 indicates that *A.tortilis* zones are found principally in the east of the home range (as suggested in Chapter 2), being associated with dryer, well-drained slopes. The denser woodlands tend to be associated with seasonal watercourses and with dams. Note that missing species (e.g *Ficus ingens*) occurred in patch sizes beyond the resolution of the habitat map. The data in

TABLE 3.1: PERCENTAGES OF HOME RANGE COVERED BY EACH HABITAT TYPE

SPECIES TYPE	DENSITY TYPE 2	3	4	5	6	7	8	TOTAL
A	0.86	9.30	13.42	0.13	0.99	1.10	0.29	26.09
B	2.92	20.65	8.40	0.80	0.28	0.27		33.32
C		0.59	3.18					3.77
D	0.63	18.69	2.77	0.01	0.12	0.06	0.11	22.39
E			0.04				0.18	0.22
F			0.06					0.06
J		0.04						0.04
K		0.10	0.15					0.25
M						0.67		0.67
N						1.09		1.09
OTHER	2.26	1.05	2.46	0.06		0.06	0.56	6.45
KOPJE								6.06
TOTAL	6.67	50.42	30.48	1.00	2.06	2.58	1.14	100

Notes: A=*Acacia etbaica*; B=*A.mellifera*; C=*A.etbaica/mellifera* mixed; D=*A.tortilis*; E=*A.brevispicata*; F=*Lycium europaeum*; J=*A.nilotica*; K=*Commiphora coricea/schimperi mixed*; M=*A.xanthophloea*; N=*A.seyal*.
2=Open; 3=light bush; 4=thick bush; 5=forest; 6=forest along watercourse; 7=thick bush along watercourse; 8=light bush, stony ground.

FIGURE 3.1: HABITAT MAP

See Table 3.1 (P.48) for legend to key

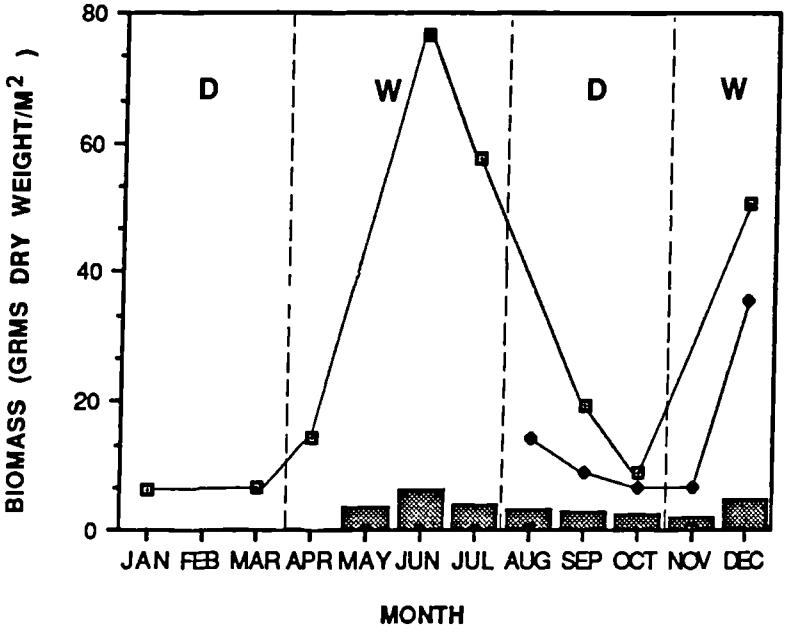
Table 3.1 are used to calculate habitat selection ratios in section 5(ii).

3. SEASONAL VARIATION IN FOOD AVAILABILITY

Estimates of food availability during the study period are plotted in Figures 3.2 and 3.3. In the first graph, three types of biomass estimate are shown; the total biomass of green herb-layer vegetation on grassland plots (six-weekly pin-frames, courtesy of U.N.B.P., January-December), the total biomass of green herb-layer vegetation on transects (monthly pin-frames, August-December), and the biomass of baboon foods (monthly quadrats, May-December). In Figure 3.3, the quadrat data are replotted on a larger scale, for greater clarity, and divided into the protein and non-protein components.

Preliminary inspection suggests that rainfall was a strong influence on biomass of both total herb-layer vegetation and of baboon foods - herb-layer biomass peaked in June, in the second half of the rainy season, then declining until the start of the short rains in November. Biomass of baboon foods, sampled over a shorter period, shows the same pattern of decline during the dry season (August-November) followed by an increase during the short rains. On average, baboon food biomass was greater in wet months than in dry months (Figure 3.4), though the difference is not quite significant ($t=2.54$, $df=4$, $p=0.064$). However, when protein biomass alone is considered, the difference is significant ($t=3.08$, $df=4$,

FIGURE 3.2: VARIATION IN BIOMASS OF TOTAL HERB-LAYER VEGETATION AND BABOON FOODS



D=Dry season
W=Wet season

■ U.N.B.P. PIN-FRAMES
● TRANSECT PIN-FRAMES
▩ QUADRATS

Pin-frames measure total herb-layer green biomass (6-weekly, Jan-Dec). Quadrats measure total available baboon food (monthly, May-Dec).

FIGURE 3.3: VARIATION IN TOTAL AND PROTEIN BIOMASS OF BABOON FOODS

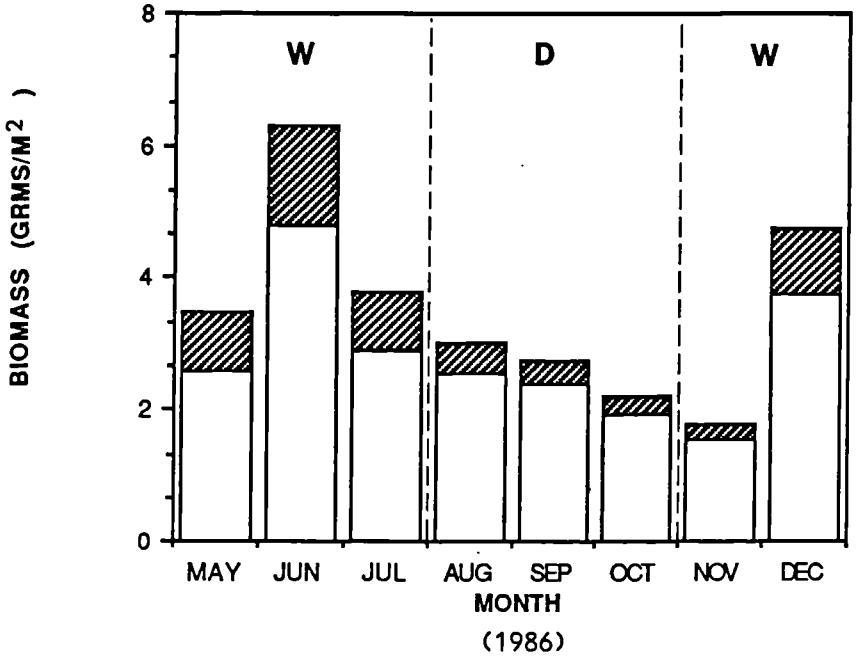
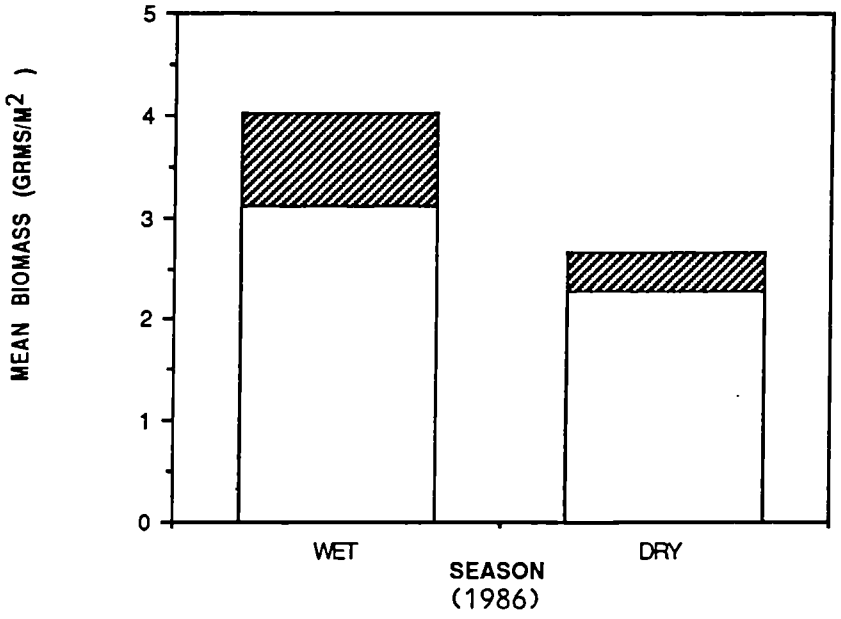


FIGURE 3.4: SEASONAL DIFFERENCE IN TOTAL AND PROTEIN BIOMASS OF BABOON FOODS



Average dry weight and protein weight of baboon foods in 5 wet and 3 dry season months (methods as in Figure 3.3).

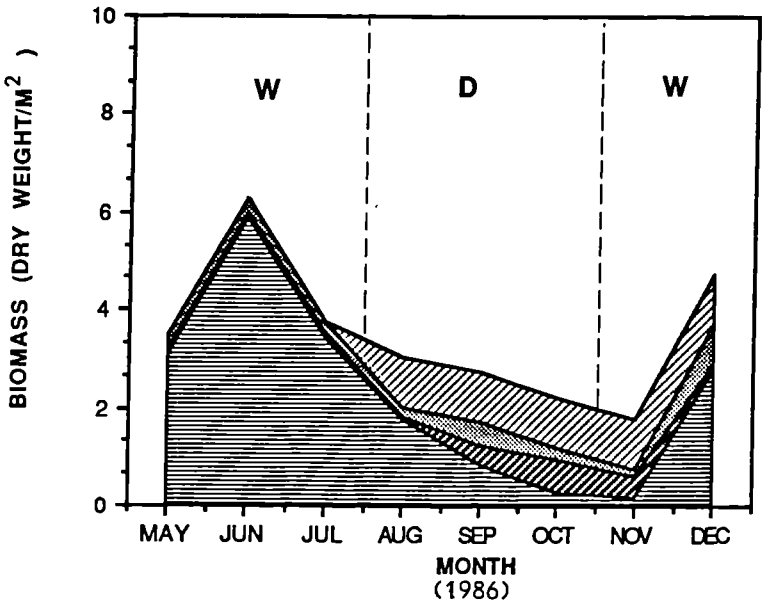
p=0.037). It is therefore possible to confirm that variation in food availability conforms to the common assumption of dry season scarcity and wet season abundance. Nevertheless, the overall difference is perhaps not as clear-cut as might be expected, and this is apparently because a time-lag effect slightly complicates the picture: November was the month of lowest food availability despite ranking third out of the eight months in terms of total rainfall. Conversely, December, which had less rain than November, ranked second overall in terms of baboon food biomass. This is not surprising because sampling was carried out in the middle of each month, so the effect of each month's rainfall could only be partially apparent in the corresponding biomass estimate. The correlation between baboon food biomass and monthly rainfall (r=0.588, df=6, p=0.069) is not as strong as that between the former and rainfall in the *previous* month (r=0.607, df=6, p=0.055). There is also likely to be a cumulative effect of rainfall, wherein biomass gradually increases as plants continue to grow and produce reproductive parts: indeed, the correlation between biomass and the rainfall total for the previous *two* months is stronger still (r=0.670, df=6, p=0.035).

In comparing the pin-frame and quadrat data, it is clear that total herb-layer green biomass while being considerably greater (especially on grassland plots), follows the same pattern of seasonal variation as the more fine-grained baboon food biomass estimates. There is a high correlation between quadrat data and the pin-frame data taken at the same plots for the period August-December (r=0.970, df=3, p=0.003). This

suggests that the major factor in the availability of baboon foods is the condition of the herb-layer, a notion supported by inspection of Figure 3.5, which shows that variation in fresh herb-layer foods (grass blades, herb leaves, shoots, flowers and fruits) effectively swamps variation in other foods; in the wet season, by far the majority of the biomass was made up of this element, and when it died back in the dry season, the availability of foods like *Acacia* flowers and pods, which are less tied to immediate rainfall patterns, was not sufficient to compensate.

As noted in Chapter 2, I have made the rather unrealistic assumption that *Cyperus blysmoides corms,* a major dry season food, are available only in months when they were eaten substantially (more than 1% of time spent feeding). Thus, in the biomass estimates, corms only contribute to the totals in five out of eight months (August-December), three of which were dry season months. There is a possibility that corm availability actually changed very little, and that the baboons simply became less selective in the dry season. However, corms were eaten in December, when overall food availability was high, suggesting that a reduction in selectivity cannot be the only reason for corm eating. Nevertheless, it is worth examining the effect of relaxing the assumption that corms were available only in months when eaten. The main effect would be to increase the wet season/dry season disparity, thereby strengthening the case for the importance of rainfall. Similarly, if the assumption that corm availability did not decrease through depletion during the dry season was relaxed, this would also increase

FIGURE 3.5: VARIATION IN COMPONENTS OF BIOMASS OF AVAILABLE FOOD

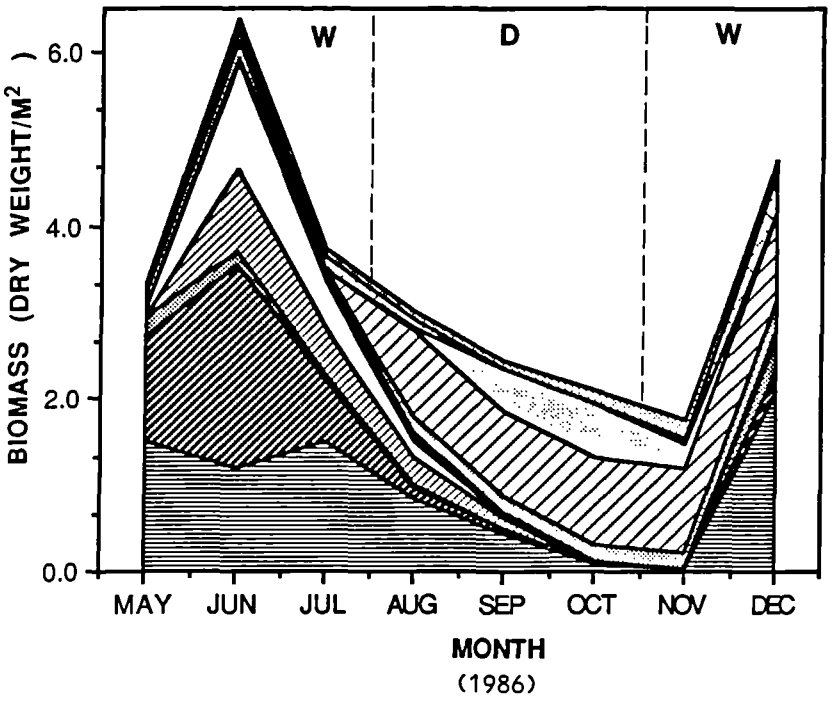


W=Wet season
D=Dry season

CORMS
TREES AND SHRUBS
HERB-LAYER (DRY)
HERB-LAYER (FRESH)

Area graph displaying monthly variation in major components of baboon food biomass (methods as for Figure 3.3).

FIGURE 3.6: VARIATION IN AVAILABILITY OF FOOD TYPES



W=Wet season
D=Dry season

- OTHER
- ACACIA SEEDS/PODS
- ACACIA FLOWERS
- CORMS
- SEDGE BASES
- HERB FLOWERS
- SHRUB FRUITS
- HERB FRUITS
- GRASS SEEDHEADS
- SHRUB LEAVES
- HERB LEAVES
- GRASS BLADES

Area graph displaying monthly variation in biomass of major food types (methods as for Figure 3.3).

the disparity. In summary, the simplifying assumptions made are conservative with respect to the dichotomy between dry season scarcity and wet season abundance, though this obviously does not help us to understand the observed variation in corm consumption.

The general validity of the wet/dry dichotomy might be challenged on the basis that the period for which baboon foods were sampled was only eight months - not even a full annual cycle. Things might be different in the long dry season (January-March), or in different years. What if some dry seasons see the simultaneous production of large amounts of *Acacia* flowers and pods, for example? Two main arguments can be advanced against this. Firstly, it appears that the phenology of other plants is also to some extent affected by immediate rainfall patterns. Table 3.2 displays correlations between the biomass of particular food types and rainfall (a) for the same month, (b) for the previous month, and (c) for the previous two months. It can be seen that rainfall has a strong impact on herb-layer foods as expected, but also to an extent on production of shrub leaves. The correlations between biomass and rainfall in the previous two months are positive, though not significant, for shrub fruits and *Acacia* leaves. These trends will tend to emphasize the impact of rainfall. The only significant negative correlation is between biomass of *Acacia* flowers and rainfall in the previous month, reinforcing the impression that these are produced mainly in the dry season. This could be the result of a longer time-lag, with rainfall stimulating the initiation of reproductive cycles which culminate in the production of

TABLE 3.2: PEARSON CORRELATIONS BETWEEN RAINFALL AND BIOMASS OF BABOON FOODS

	MONTH		
	SAME	PREVIOUS	PREVIOUS TWO
TOTAL BIOMASS	0.587	0.617*	0.670*
HERB/GRASS FOLIAGE	0.793**	0.889**	0.815**
HERB FRUITS	0.640*	0.561	0.803**
HERB FLOWERS	0.381	0.554	0.795**
SHRUB FOLIAGE	0.370	0.595*	0.172
SHRUB FRUITS	-0.404	-0.043	0.349
ACACIA FLOWERS	-0.541	-0.635*	-0.547
ACACIA PODS	-0.041	0.153	0.031
ACACIA FOLIAGE	-0.036	0.440	0.385
	* $p<0.05$	** $p<0.02$	

flowers and pods some months later. This idea is supported by the observation that production of *A.etbaica* flowers failed almost entirely in September 1987 following poor rains (D.Lochhead, unpublished data).

Given that the production of *Acacia* reproductive parts is by no means restricted to the wet season, what is the likelihood that in some dry seasons, in particular the long dry season between January and March, these compensate for the paucity of herb-layer and other vegetation? Firstly, data from the year following my study do not support this idea (D.Lochhead, in prep.). Secondly, in the long dry season of 1986, *A.mellifera* and *A.tortilis* both flowered and then produced seed pods, but asynchronously, and *A.mellifera* pod production did not peak until the following wet season (information from field notes).

A.etbaica did not flower. Thus, at no time was there a single synchronised peak of production that could have made a substantial difference to the conclusion that dry seasons are times of relative scarcity.

4. IMPLICATIONS OF SEASONALITY FOR BABOONS

I have argued that food availability for the study troop was strongly related to patterns of rainfall distribution. This will perhaps come as no surprise to savannah ecologists, since

> " It is well known that there is a relationship between rainfall and primary production in arid and savannah habitats " (Delaney and Happold, 1979).

However, this is the first formal demonstration that the relationship applies within the range of items eaten by baboons. I do not wish to overstate the case for a simple distinction between wet and dry seasons; after all, the definition of seasons is arbitrary, and, as we have seen, there are time-lag effects whose magnitude probably varies according to the type and size of plant (new grass growth appears within one or two weeks of the onset of rain, while *Acacia* reproductive cycles are more likely to be influenced by cumulative rainfall over a period of months, and perhaps even years).

One important implication of these findings is that they suggest that seasonal energy bottlenecks may occur. Such bottlenecks can only be validly defined in terms of effects on

baboons, and the demonstration of fluctuations in food availability does not in itself tell us much about constraints on baboons; it is possible that, even during the dry season, animals are not significantly energy-limited (Coelho *et al.*, 1976; but c.f. Cant, 1980). This could be the case, for example, if the primary regulator of population density was predation. Also, characteristic of baboons is that they are well equipped to ameliorate the effects of seasonal bottlenecks by their ability to utilise a very wide range of food types, from the tops of the trees to below ground (Altmann and Altmann, 1970; Hamilton et al., 1978; Post, 1978; Norton *et al.* 1987; Whiten *et al.*, 1987). In fact, as I will show, there are very good reasons for believing that, in STT, females in particular face significant energetic constraints which increase in severity during the dry season. This seems to be true to some extent even in a "normal" year, when there are two good rainy seasons (as during my study), minimising the extent of the dry season hiatus - there was approximately a three-and-a-half-fold difference in biomass between the months of greatest and lowest food availability. It is therefore no surprise that the effective failure of the short rains at the end of 1987 resulted in dramatically reduced body condition and increased mortality amongst adult females and their infants (I.Saunders, unpublished data). It is possible that such droughts are a factor of major importance in the ecology and population dynamics of these baboons.

The use of space and time are central considerations in the evaluation of ecological constraints acting on animals (MacArthur and Pianka, 1966; Altmann, 1974; Krebs, 1978). An

important implication of variation in the density of food available in the environment is that the size of the harvesting area needed to satisfy nutritional requirements will be affected. This parameter can be estimated using information on food requirements (defined here as daily intake rates - see Chapter 7 for further details) and food availability. Data for the two months of highest and lowest biomass are presented in Table 3.3, and indicate that in the poorest month, each adult female would have to harvest an area of 232 m^2 per day in order to satisfy her food intake requirements. With an average of 228 minutes per day devoted to feeding, she would have to harvest all the food items from an area of 1.023 m^2 each minute of her feeding time. The corresponding figures for the best month are a daily harvest area of 68 m^2 and a per-minute of feeding time harvest area of 0.263 m^2.

TABLE 3.3: ESTIMATION OF REQUIRED SEARCH AREAS FOR AN ADULT FEMALE IN BEST AND WORST MONTH

MONTH	DAILY INTAKE[1]	BIOMASS[2]	TIME FEEDING[3]	DAILY HARVEST AREA[4]	HARVEST AREA PER MINUTE[5]
JUNE	427.5	6.286	258	68.01	0.263
NOVEMBER	413.6	1.781	228	232.20	1.023

Notes: [1] Mean dry weight intake (g/day); [2] Baboon food biomass (g/m^2 dry weight); [3] Mean time feeding (mins/day); [4] Estimated required daily harvest area (m^2/day); [5] Estimated required harvest area per minute of feeding time (m^2/minute).

The biomass figures represent average food availability for the whole home range, and since it is highly likely that the baboons select foraging areas according to the density of

resources, the data in Table 3.3 probably overestimate required harvest areas, and hence time-budgeting constraints. Set against this, however, is the certainty that individuals do not harvest every item within the area in which they forage; some are inevitably missed, and some may be rejected because they are nutritionally sub-optimal in terms of what else is available and what else is needed to balance the animal's diet that day. Because of these factors, it is not possible to assess the absolute accuracy of the harvesting area estimates, but the data serve to emphasise the likely effects of variation in food availability on ranging and activity budgets. Note, however, that the prediction of a seasonal difference in the harvesting area needed to satisfy intake requirements depends on the assumption that overall changes in biomass are at least partly a function of changes in the density of food items within patches, and not simply of a reduction in the number or size of patches (this is discussed in the next section). It may seem puzzling that the amount of time spent feeding was lower in November than in June, thereby apparently further increasing the harvesting area needed for each minute of feeding time. Why did the baboons not "try harder" when conditions were worse? The answer is that they may have done; this can only be evaluated by reference to time spent *foraging*, since the feeding time budget only reflects actual manipulation and ingestion of food, not searching. This subject is taken up in Chapter 5, while seasonal variation in ranging is examined in succeeding sections of this Chapter.

5. SPATIAL DISTRIBUTION PATTERNS OF FOOD AND THE PROBLEM OF PATCHINESS

In addition to gross abundance, much attention has been devoted by primatologists to the relevance of spatial distribution patterns of foods to a number of demographic and behavioural variables. These include group size, composition and stability, territoriality, ranging patterns and inter- and intragroup social relations (e.g.Crook and Gartlan, 1966; Altmann, 1974; Clutton-Brock, 1974; Klein and Klein, 1977; Waser, 1977; Lindburg, 1977; Dunbar, 1977; Wrangham, 1977, 1980,1986; Clutton-Brock and Harvey, 1977a; Whitten, 1983). In particular these and other authors have referred to the "patchiness" of resources. However, variables such as "patchiness", "patch size" and "inter-patch distance" are notoriously difficult to quantify (Wrangham, 1983; Krebs and McCleery, 1984). It is rare that clear patch boundaries exist in natural situations, so the definition and measurement of patches will always be somewhat arbitrary and subjective. One solution to the problem of patch size is to measure the "survival time" between animals entering and leaving patches, controlling for the number of animals involved (White, 1989). The amount of time taken to exhaust patches can then be used as a measure of relative patch size, at least within a species. This approach suffers from essentially the same problem encountered in measuring a patch directly; where (and when) does the patch start and finish? The problem may be minimal for animals feeding mostly or exclusively in trees, since each separate tree can often be considered an individual patch. For baboons, which gather a great deal of their food from the herb-layer and beneath, the approach would not be

viable. Indeed, it is a moot point whether the concept of patches is a useful one at all in this context, because it seems inevitable that "patches" will tend to be contiguous, overlapping and even concentric.

These methodological and conceptual problems with patches seem to rule out comprehensive quantitative analysis involving unitary measures of patchiness. This is not to say that spatial heterogeneity is unimportant, for this or any other population of primate, nor even that attempts should not be made to assess it in some way. It is clearly crucial to understanding variation in patterns of intragroup competition, for example (see Chapter 7). Extensive investigation of seasonal variation in heterogeneity is outside the scope of this project, so this discussion will be based largely on qualitative observations supplemented by data on spatial variance in food density.

During the wet season the major food sources were grasses, herbs and shrubs, with a variable amount (0.2-10.0%) being derived from trees. In the dry season dietary diversity was lower (see Chapter 6) and the major food sources were *Acacia* trees (flowers and pods) and sedge corms (*Cyperus blysmoides*) and bases (*Mariscus amauropus*). The pads of the succulent tree (*Euphorbia nyikae*) were an important food in the first dry season.

The first point to make is that, assuming that the distribution of particular plant species is not entirely homogenous, it is reasonable to expect that a reduction in the

number of available food species will automatically result in an increase in patchiness. Secondly, wet season foods appear to be intrinsically more evenly distributed than the dry season foods; the grasses and herbs that provided the foliage, flowers and fruit eaten extensively in the wet season covered the ground almost everywhere, and in many places occurred in large meadows capable of accomodating the whole troop, even when individuals were spread widely apart. In contrast, flowering and fruiting *Acacia* trees could often be clumped in distribution because, while extensive woodlands of the three main food species occurred in many parts of the home range, the production of reproductive parts was to an extent asynchronous. This meant that "rich pickings" were frequently restricted to relatively small groves within particular areas, and even to individual trees. The leaf bases of *Mariscus amauropus* did not appear to be a clumped resource, on any scale, but the corms of the other important sedge, *Cyperus blysmoides*, did. The latter were dug almost exclusively from relatively well-defined, isolated patches of ground, between about 30 and 75 metres in diameter; these "corming sites" appeared to occur at the old and long-disused sites of settlement by nomadic pastoralists. Finally, specimens of *Euphorbia nyikae* occurred in fairly large clumps, mostly associated with kopjes and other rocky outcrops, and were entirely absent from large tracts of the home range.

A more formal way of examining these trends is to compare the average biomass for the home range with the <u>maximum</u> biomass within food patches. I have estimated the latter by extracting data for individual herb-layer quadrats (0.25 m^2)

and for individual trees. The month of greatest average biomass, at the height of the wet season, was June, with 6.286 g/m^2; the maximum biomasses at this time, recorded from the top two quadrats, were 40.588 g/m^2 and 32.374 g/m^2. Thus, within-patch biomass was 5-6.5 times greater than the average biomass. Assuming that fresh herb-layer vegetation made a negligble contribution to the biomass and diet at the height of the second dry season (see Figure 3.6 and Chapter 6), it is valid to concentrate on *Acacia* products and corms for this period (biomass data are not available for the first dry season). Within patch-biomass of *Acacia* flowers is obtained by

$$\text{Biomass} = wn/a$$

where w is the dry weight of the average flower, n is the number of flowers in the tree and a is the canopy area of the tree (diameters of all sampled trees were measured when transects were established).
The two greatest recorded within-patch biomasses for *A.etbaica* flowers in September (approximately 60% of the diet) were 38.011 g/m^2 and 36.256 g/m^2 (13.2-13.8 times greater than the average). For *A.tortilis* flowers (30% Of the diet in October) they were 35.774 g/m^2 and 32.386 g/m^2 (14.6-16.2 times greater than the average). The average biomass of corms of *Cyperus blysmoides* at sites used by the baboons was 42.901 g/m^2 (14.1-19.4 times the overall biomass during dry season months).

These data suggest seasonal variability in the extent to which available resources were spatially clumped; although overall biomass was up to 3.5 times greater in the wet season than in

the dry season, the maximum biomass within patches of the most important foods was actually very consistent.

So far no attempt has been made to assess the scale of spatial heterogeneity. The significance of the observation that biomass is distributed more patchily in the dry season is difficult to interpret without knowing something about the size of patches (real or abstracted) and the distance between them. If local concentrations of biomass are large but spaced widely apart, this may affect ranging but not intragroup competition. Conversely, if such concentrations are small relative to troop size, both variables may be affected. If patches are both small and close together, then neither ranging nor competition may be significantly affected.

The solution to the problem of scale is not at all obvious. Whitten (1983) related the extent of feeding competition within troops of vervet monkeys (*Cercopithecus aethiops*) to the non-randomness of distribution of food species. She assessed the latter as the ratio of the variance to the mean number of individuals per sample point. This is a good measure of the extent to which particular species occur in clumps, but it is difficult to interpret its relevance to behaviour because it is entirely dimensionless; "clumping" by this definition is an abstract concept unrelated to the scale at which the monkeys operated. It is therefore not surprising that Whitten felt it necessary to support her arguments with qualitative descriptions. For example, in her study doum palms (*Hyphaena coriacea*) were randomly distributed according to the criterion used, yet rank-related differences in feeding

were apparent. The anomaly was explained by the observation that fruits were clumped on a smaller scale, within individual trees. This is perfectly convincing, but it serves to illustrate the problematic nature of scaleless measures of spatial heterogeneity.

Perhaps the problem of rigorous quantification is insurmountable. However, the observation that spatial heterogeneity varies between seasons, at least in an abstract sense, is a useful starting point, since it allows for the *possibility* that behaviour is affected, although from this point on I am restricted to subjective evaluations. What evidence is there that increased patchiness in the dry season was of a scale that would influence (a) ranging, and (b) intragroup feeding competition?

My strong impression was that, during the dry season, more time was spent by the baboons traveling between localised food sources such as *Acacia* groves, corming sites and waterholes, with little or no feeding on the way. In the wet season, bouts of feeding and moving appeared less distinguishable, the large expanses of herb-layer greenery providing a rich substrate for continuous "travel-feeding" (Whiten *et al.*, 1987). The data already presented on within-patch biomasses suggest that, contrary to the conclusions derived from Table 3.3, the required harvesting areas would not necessarily increase as average biomass decreased. Therefore, seasonal changes in day range length, evaluated in the next section, are most likely to be principally related to effects on the between-patch travel component.

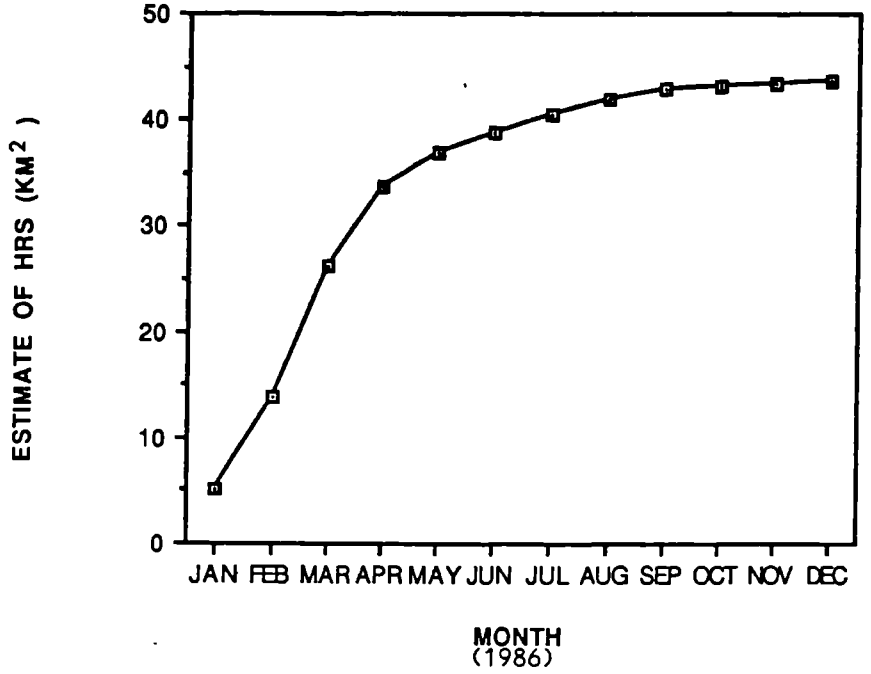
With respect to intragroup interactions, there is also evidence that "effective" patchiness increased during the dry season, resulting in greater levels of competition. Some of the groves of flowering *Acacias* visited by the baboons were extensive, with many trees simultaneously in flower. Others, however, comprised just a few trees, often with one or two larger individuals plainly being the richest source of food, and attracting high densities of baboons. Fallen flowers, which accumulated on the ground in small drifts, were also eaten. As already mentioned, corms of *Cyperus blysmoides* were concentrated in relatively discrete patches 30-75 metres in diameter - not large relative to the size of the troop - and spatial clustering of feeding animals was greater for this food than for any other. Seasonal differences in feeding competition and their relationship with resource characteristics are explored further in Chapter 7.

6. PATTERNS OF RANGING AND HABITAT USE

(a) Home range size

The size of the home range (HRS) was estimated by summing the total number of $^1/_4$ km^2 quadrats entered throughout the 12-month study period (January-December, 1986). These formed a coextensive block, enclosing only one quadrat which was never seen to be entered. The HRS given by this method was 43.75 km^2. To check that this estimate represents the asymptotic function of study time, I have plotted the cumulative estimate obtained for each month in the method of Sharman (1981). This shows that the final estimate does indeed represent a near-

FIGURE 3.7: MONTHLY CHANGES IN HOME RANGE SIZE ESTIMATES

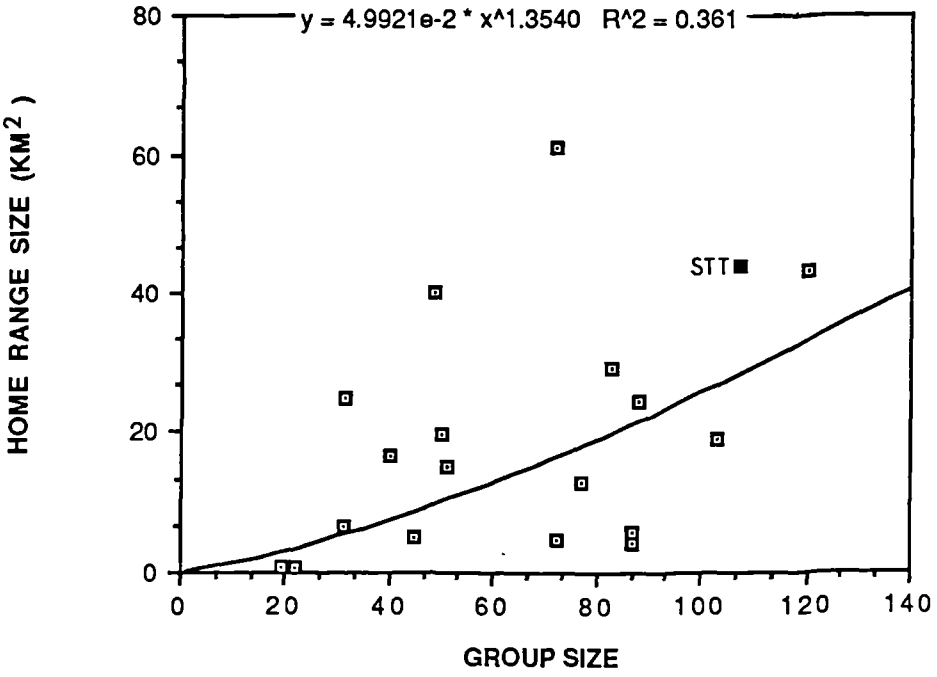


Cumulative home range size estimated by summing the area of quadrats entered by the end of each month.

asymptotic value, vindicating the assumption that the study duration was sufficient to yield a reliable HRS, at least given the general ecological conditions, population density and group size in the study period. Of course these variables are not entirely static and, indeed, when STT split during a drought in 1987, HRS changed substantially for at least one of the sub-groups (D.Lochhead, in prep.).

The HRS of 43.75km^2 is certainly large compared to other populations, and this is true even when group size has been taken into account. In Figure 3.8 I have plotted the HRS of 19 populations of *Papio* baboons against their respective group sizes, and fitted the curve for the logarithmic function of the relationship (which gives a better fit than a straight line, while preserving the original scale for ease of interpretation). Data were extracted from Sharman (1981) and Sharman and Dunbar (1982) - the value for *P.papio* was not included because the extremely large group size of 247 conceals the fact that troops split into smaller parties while foraging, and because the asymptotic HRS was not known (Sharman, 1981). Thirty-six percent of the variance in home range size is explained by the regression. It can be seen that the value for STT falls somewhat above the line, implying a larger HRS than expected. However, caution should be exercised in interpreting this result given the relatively small sample size and a certain diversity of methodology underlying the published estimates.

FIGURE 3.8: RELATIONSHIP BETWEEN GROUP SIZE AND HOME RANGE SIZE IN PAPIO BABOONS



Data from Sharman and Dunbar (1982): 18 populations plus STT. Best-fit curvilinear regression determined using "CRICKET" graphics package.

(b) Mean day range length

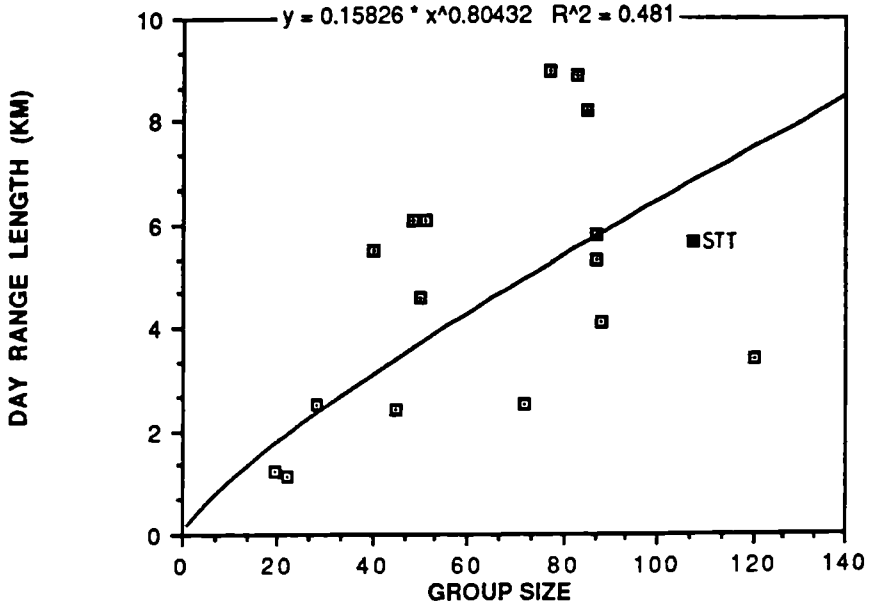
The mean day range length (DRL) for the 12-month study period, calculated as the mean of monthly means, was 5.637 km (standard deviation=1.553). In Figure 3.9 the mean DRL is plotted against group size for STT and 16 other populations of *Papio* baboons, using the same sources of data and curve-fitting procedure as for HRS. This shows that the DRL is significantly related to group size, a result also obtained by Sharman and Dunbar (1982), with 48% of the variance explained. The DRL obtained for STT is clearly not grossly unusual for a troop of its size.

The mean value actually conceals a bimodal distribution of DRLs; the distances travelled on days when the baboons changed sleeping sites was significantly greater than when they returned to the same sleeping site ($t=^{-}2.91$, df=9, p=0.017; mean return DRL = 5071 m., mean intersite DRL = 6480 m.). This needs to be taken into account in the interpretation of seasonal differences in DRL.

(c) Seasonal variation in day range length

Day range length varied significantly between months (Kruskal-Wallis test; H=23.09, df=7, $p<0.01$), though the overall difference between wet months and dry months was not significant (t=1.89, df=7, p=0.103). As noted in section 3.3, the simple wet/dry dichotomy reflects seasonal variation in food availability imperfectly, at least in part because of time-lags between rainfall and biomass peaks. Accordingly, I have calculated correlations between day range length and the

FIGURE 3.9: RELATIONSHIP BETWEEN GROUP SIZE AND DAY RANGE LENGTH IN PAPIO BABOONS



Data and methods as for Figure 3.8.

following variables: monthly rainfall, rainfall for previous two months, total herb-layer green biomass and baboon food biomass. Sample sizes vary according to the following constraints: ranging and rainfall data are available for twelve separate months; herb-layer biomass data (grassland pin-frame plots) are also available for the whole period, but only as six-weekly measurements (n=7), and it was therefore necessary to calculate mean day ranges for the equivalent intervals; baboon food biomass data are available only for eight separate months. Correlation coefficients are displayed in Table 3.4.

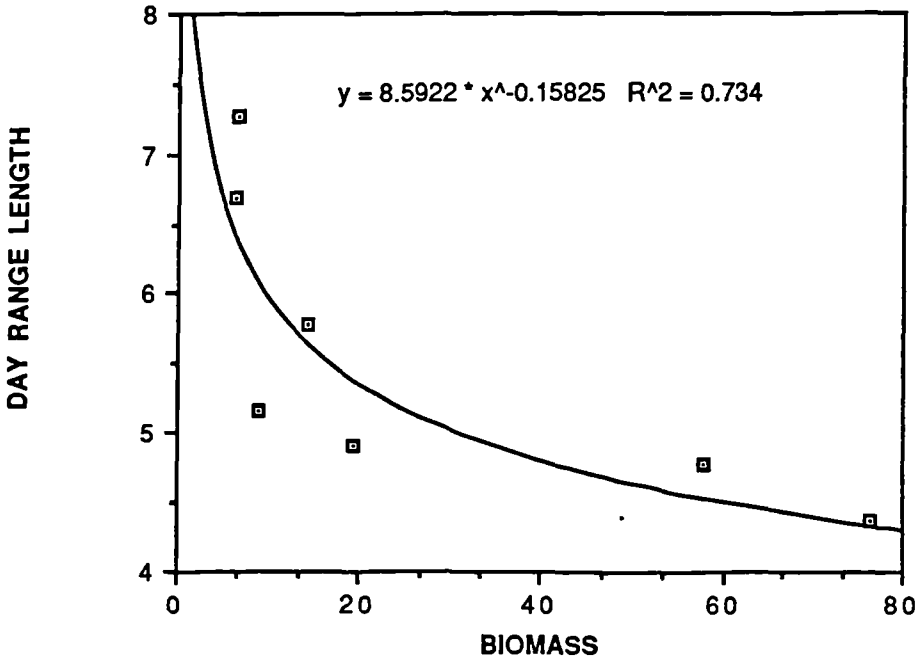
TABLE 3.4: ENVIRONMENTAL CORRELATES OF DAY RANGE LENGTH

	r[1]	n	Period
1.RAINFALL			
a)Monthly	0.230	12	12 MONTHS
b)Previous 2 months	-0.536*	12	12 MONTHS
2.TOTAL GREEN BIOMASS			
a)All day ranges	-0.917**	7	12 MONTHS
b)Return day ranges[2]	-0.825**	7	12 MONTHS
c)Intersite day ranges[3]	-0.791*	7	12 MONTHS
3.BABOON FOOD BIOMASS			
a)All day ranges	-0.467	8	8 MONTHS
b)Return day ranges[2]	-0.510	8	8 MONTHS
c)Intersite day ranges[3]	-0.412	8	8 MONTHS

Notes: [1] Pearson correlation coefficients
[2] Return to same sleeping site [3] Move sleeping site
* P<0.05 ** P<0.01

There is a highly significant negative correlation between total green biomass and DRL, and this correlation holds when the data are split into "return" and "intersite" day ranges. As a corollary to this, there is no significant correlation between the total green biomass and the proportion of intersite day ranges ($r=0.290$, $df=5$, $p>0.05$). Thus the

FIGURE 3.10: RELATIONSHIP BETWEEN TOTAL HERB-LAYER GREEN BIOMASS AND DAY RANGE LENGTH



Data points are means of day journeys for 7 six-weekly periods in 1986; herb-layer green biomass measured by pin-frame method, regression determined using "CRICKET" graphics package.

observed variation in DRL is not simply a function of changes in the frequency with which the baboons moved to new sleeping sites. Instead, the baboons showed a general tendency to travel further when biomass was low, supporting the prediction made in the previous section. However, the difference between the average DRLs in the two most extreme periods is only about half that predicted by the difference in biomass - it will be recalled that biomass in the "best" month was about 3.5 times greater than that in the "worst" month, whereas mean DRL differed only by a factor of about 1.6 (7.4 km vs 4.3 km).

The fact that a significant negative correlation exists between rainfall for the previous two months and DRL, but not for monthly rainfall and DRL, lends further support to the notion of a time-lag effect. The correlations with baboon food biomass are negative, but not significant, a fact which may seem surprising given that this parameter is theoretically a measure of more direct relevance to the behaviour of the baboons than is total herb-layer green biomass. However, it must be remembered that baboon food biomass was only sampled for the last eight months of the study, entirely missing out the relatively extreme conditions of the first dry season.

The data suggest that, through their direct influence on food availability, rainfall patterns were an important determinant of ranging. This notion can be pursued further by analysis of comparative data. The question is whether the longitudinal patterns of temporal covariation in this population are mirrored by patterns of interpopulation covariation. The assumption needs to be made that, just as seasonal rainfall

patterns determine variation in biomass, differences between study sites in mean annual rainfall reflect differences in mean annual productivity. This is a reasonable assumption (Phillipson, 1975; Delaney and Happold, 1979), though there are obviously other factors that are also likely to influence productivity. As we have seen, DRL is significantly related to group size (Sharman and Dunbar,1982, and analysis above), so it is desirable to control for the latter variable in assessing the relationship between DRL and rainfall. Once again using data from Sharman and Dunbar (*op cit.*), I have carried out a multiple regression with log DRL as the dependent variable and log rainfall and log group size as the independent variables. A summary of the results is presented in Table 3.5.

TABLE 3.5: MULTIPLE REGRESSION ANALYSIS OF INTERPOPULATION VARIATION IN DAY RANGE LENGTH

INDEPENDENT VARIABLE	BETA*	T	SIG T
Rainfall	-0.589	-3.04	0.008
Group size	0.654	4.07	0.001

$F=13.32$ $df=14$ $p<0.001$ adjusted $r^2=0.625$

Notes: * standardised regression coefficient

The regression is highly significant, with 62% of the variance in DRL explained. DRL is independently related to rainfall (negatively) and group size (positively). Thus, both seasonal patterns observed in the study of STT, and variation between study populations, support the contention that baboons have to travel further each day to find sufficient food when availability is low.

(d) Discussion of day range length variation

It has been established that the distance travelled by the baboons each day varied significantly between months, and that this variation correlates with changes in food availability, itself related to rainfall patterns. The initial hypothesis suggested to explain the relationship between DRL and biomass was that the harvesting area needed to satisfy nutritional requirements is directly proportional to the average density of food within the home range. However, it was subsequently found that food density within the most productive patches was substantially similar during the months of highest and lowest biomass, and therefore that changes in biomass are to a great extent a function of changes in the spatial uniformity of food distribution, rather than in overall food density. Thus, it appears that increased patchiness of resources in the dry season is the main reason for day ranges being longer, although comprehensive data on spatial heterogeneity of resources are required before this issue can be completely resolved.

Dry season food patches, such as flowering *Acacias* and corming sites, are likely to be less diverse sources of nutrients than comparably-sized feeding areas in the wet season. In general, there seemed to be a greater tendency for particular areas to be visited for specific food types in the dry season, with the whole troop sometimes spending several hours exploiting essentially one food. The situation was rather different in the wet season, when a large number of different foods

(foliage, flowers, fruits and sometimes invertebrates) were available in relatively small areas of the herb-layer, and there would presumably have been less need to move on to entirely new feeding areas. This seems to have been the case, since it was not an infrequent occurrence at this time for the troop to spend the whole day within about one kilometre of the sleeping site. Water was more widely available during the wet season, both because foods contained more, and because temporary rain pools were abundant. The main sources of water in the dry season (dams on Chololo Ranch and holes dug in the sandy beds of dry watercourses) were localised, and this could have been an additional pressure forcing the baboons to travel further each day.

There has been a considerable lack of uniformity in the results of studies examining seasonal variation in day range lengths of primates. Several studies, including two on *Papio* baboons, found no significant seasonal variation (*Papio cynocephalus*; Post, 1978: *Papio papio*; Sharman, 1981: *Cercocebus albigena*; Waser, 1977: *Indri indri*; Pollock, 1977). Two studies of baboons, including this one, and two on other Old World monkeys, have reported a negative association between DRL and food availability, although the latter is invariably inferred , rather than measured (*Papio anubis*; Lee, 1983, and this study: *Macaca mulatta*; Lindburg, 1977: *Colobus badius*: Clutton-Brock, 1975). Altmann and Muruthi (1988) found that DRL of a semi-provisioned troop of yellow baboons (*Papio cynocephalus*) was significantly less than that of wild-feeding groups. A study of Sifakas (*Propithecus verrauxii*) found that DRL was lower when food was assumed to be <u>less</u>

abundant, in the dry season (Richard, 1977). Chivers (1977) and Bennett (1986) also suggested that DRL was reduced when food was scarce, in studies of siamang (*Symphalangus syndactylus*) and banded langurs (*Presbytis melalophos*) respectively, but in the latter case it appeared that abundance was positively correlated with patchiness. Two studies, both on New World monkeys, have argued specifically that DRL increased in seasons when food was most clumped (*Brachyteles*: Strier, 1987. *Saimiri sciurus* and *Cebus*: Terborgh, 1983) though, as in this study, differences in spatial distribution patterns were inferred rather than directly measured.

There is plainly a need for a more quantitative approach to the evaluation of ecological influences on ranging, with respect to both seasonal variation and differences between populations and species. From the evidence available to date it seems that DRLs are probably strongly related to patchiness of resources, with overall availability perhaps being a secondary factor (Lee, 1983). Where seasonal variation in baboons has been observed, DRL seems to be negatively associated with availability, and perhaps positively with patchiness. However, until these variables are properly quantified it will be impossible to confidently evaluate their relative importance.

(e) Habitat use

There have been many studies relating differential use of areas of the home range to resource distribution. Waser

(1977) found that the areas used most intensively by mangabeys (*Cercocebus albigena*) were centred on fruiting trees. Lindburg (1977) identified water sources as the most important determinant of differential range use by rhesus monkeys (*Macaca mulatta*). Seasonal shifts in range use have been related to food availability in gelada *Theropithecus gelada* (Dunbar, 1977), chimpanzees *Pan troglodytes* (Wrangham, 1977) and mountain gorillas *Gorilla g. berengei* (Goodall, 1977). These are just a few of the published observations, but little would be gained by multiplying examples. Importantly, however, there seems to have been a singular lack of formal statistical treatment, arising perhaps from a certain reluctance to quantify the relevant ecological and habitat variables. Instead, authors have generally relied on qualitative assessments of associations between range use and resource distribution. While this may be sufficient in many cases for interpreting gross patterns of range use, the approach is extremely limited when it comes to evaluating the importance of a number of influences, and there will always be the danger posed by confounding variables. With regard to studies of baboons, there are at least three exceptions, in which attempts were made to separate the influences of environmental variables (Post, 1978; Sigg and Stolba, 1981; Stelzner, 1988). The results of these studies will be discussed alongside the following analyses.

The habitat types used for the analyses are as defined in Chapter 2 and quantified in Table 3.1. The approach taken is to consider habitat use according to species dominance and tree/shrub density independently, and to then assess whether

the observed influences of these factors are genuinely independent of one another. It is important to distinguish between the overall *importance* of particular habitat types, in terms of the time spent within them (time-habitat budgets), and the extent to which they are *selected* (evaluated by taking relative abundance into account). These two issues are considered separately below.

(i) Summary of time-habitat budgets

The percentage of time spent in each habitat type, calculated from focal point samples, are presented in Table 3.6. Equivalent density categories (3 and 8, and 4, 7 and 9 - see Figure 2.1) have been collapsed, since some of these represent only very small proportions of the home range. Note also that some of the minor species/density sub-types occupied do not appear in the habitat breakdown (Table 3.1), due to the relatively low resolution of the habitat map. Because of this lack of resolution, detailed consideration of use of species types is restricted to the three major ones - *Acacia etbaica*, *A.mellifera* and *A.tortilis*. The following observations can be made:

(a) The three most abundant species types were also the three most occupied, together accounting for 78% of the animals' time.

(b) Nearly half the animals' time was spent in *A.etbaica* habitats.

(c) Similarly, the two most abundant density types (light and thick bush) were the most frequently occupied, together accounting for 74% of the animals' time.

TABLE 3.6: PERCENT OCCUPANCY OF HABITAT TYPES

SPECIES TYPE	DENSITY TYPE 2	3/8	4/7/9	5/6	OTHER	TOTAL
A	1.51	17.36	18.44	4.39	0.84	42.54
B	1.68	16.35	6.62	0.85	0.23	25.73
C	0.05	0.64	0.22			0.91
D	1.20	6.13	2.75	0.11	0.13	10.32
E	0.04	0.59		0.10	1.30	2.03
F	0.14	0.28		0.21		0.63
J	0.63	2.32	0.80	0.09	0.18	4.02
K	0.03	0.37	0.01	0.02	0.34	0.77
M			0.36	0.62	0.45	1.43
N			0.13			0.13
OTHER	0.15	0.55		0.53	10.96	12.19
TOTAL	5.43	44.59	29.33	6.92	14.43*	100

Notes: * Includes 6.19% in type 10 (kopjes). A=*Acacia etbaica*; B=*A.mellifera*; C=*A.etbaica/mellifera* mixed; D=*A.tortilis*; E=*A.brevispicata*; F=*Lycium europaeum*; J=*A.nilotica*; K=*Commiphora coricea/schimperi mixed*; M=*A.xanthophloea*; N=*A.seyal*. 2=Open; 3=light bush; 4=thick bush; 5=forest; 6=forest along watercourse; 7=thick bush along watercourse; 8=light bush, stony ground; 9=thick bush, stony ground.

(d) Reference to Table 3.1 suggests that species type and density type are confounded (most *A.etbaïca* habitat is thick bush, whereas most *A.mellifera* and *A.tortilis* habitat is light bush).

Thus, in terms of the overall time-habitat budgets, medium-density zones (light and thick bush) dominated by *A.etbaica*, *A.mellifera* and *A.tortilis* were the most important types. However, because species dominance and density are confounded, interpretation of the patterns of habitat selectivity demands that each variable be controlled in considering the influence of the other.

(ii) Habitat selectivity

In order to examine selectivity in habitat use, observed frequencies of occupancy of habitat types are compared with frequencies expected on the basis of their relative abundance (percentage of the home range). Selection ratios (% time divided by % area) are presented in table 3.7, and the separate influences of species dominance and tree density on habitat selection are considered below. Statistical analyses of the influence of species dominance are restricted to the three major types (see Table 3.1 for key).

TABLE 3.7: HABITAT SELECTION RATIOS

	DENSITY TYPE				
SPECIES TYPE	2	3/8	4/7/9	5/6	TOTAL
A	1.76	1.81	1.27	3.92	1.63
B	0.58	0.79	0.76	0.79	0.77
D	1.90	0.33	0.97	0.85	0.46
TOTAL	0.81	0.87	0.89	2.26	1.00

Species dominance: Frequencies of occupancy of different species types departs significantly from those predicted on the basis of relative abundance (X^2=39.2, df=7, p<0.001; only one point from each focal sample used, to preserve independence). Table 3.7 shows that *A.etbaica* habitats were positively selected, while *A.mellifera* and *A.tortilis* habitats were occupied less frequently than expected. The consistency of these patterns across density types, at least for *A.etbaica* and *A.mellifera*, suggests that patterns of selectivity are not simply a result of the confounding effects of selectivity for correlated density types. When observed and expected frequencies are analysed using the Wilcoxan matched-pairs signed-ranks test (Siegel, 1956), the trends are consistent enough across density types to be significant for *A.etbaica* (T=0, n=7, p<0.05) and *A.mellifera* (T=1, n=7, p<0.05), but not for *A.tortilis* (T=5, n=7, p>0.05). However, the overall selection ratio for the latter habitat was the smallest of the three major types, because of the particularly low frequency of occupation of the abundant *A.tortilis*-dominated light bush (see Tables 3.1 and 3.6). In contrast, *A.tortilis*-dominated open habitat was strongly positively selected. Whether this represents a genuine case of interaction between the effects of species dominance and density, or simply error in measurement of the relative abundance of density types within the category of *A.tortilis* habitats, is not known, but in the absence of supporting evidence, it is probably safest to assume the latter.

Tree/shrub density: Frequencies of occupation of different density types also departed significantly from those predicted

from relative abundance (X^2=25.6, df=4, p<0.001; one point from each focal sample). The data in Table 3.7 suggest that overall selection ratios are positively correlated with density (r_s=1.0, which, according to Siegel (1956), can be considered as significant at the 5% level with a sample size as small as four). However, deviations of observed from expected occupancy were consistent enough across species types to be significant only in the case of positive selection for forested zones (open;T=6, n=6, p>0.06: light bush;T=19, n=8, p>0.05: thick bush; T=15, n=8, p>0.05: forest; T=6, n=9, p<0.05). Therefore, the apparent association between density and selection may be partly due to the confounding effect of species composition, though this cannot explain the preference for forested habitat.

Kopjes: As noted, kopjes constituted a distinct habitat type, and no attempt was made to sub-classify them according to species dominance or tree/shrub density. Occupancy was at almost exact parity with abundance (selection ratio=1.02).

(iii) Determinants of habitat selectivity

In the preceding section, an overall preference for *A.etbaica*-dominated habitat, and a positive association between selectivity and tree density were noted. A number of possibilities need to be considered in trying to explain these preferences. Firstly, preference for particular species types might reflect intensive dietary utilisation by the baboons of food items from that species. Secondly, it is possible that tree-species dominance and tree density reflect

wider characteristics of the vegetational association, which bear on overall productivity. For example, *A.tortilis* trees tend to be associated with relatively dry, well-drained soils (see chapter 2), having implications for herb-layer productivity. Thirdly, there could be systematic or coincidental spatial associations between habitat types and other important features of the home range, such as sleeping sites and water sources (see for example Sharman, 1981; Sigg and Stolba, 1981; Lindburg, 1977; Post, 1978; Crompton and Andau, 1987; Chapman, 1988). Finally, as a "last resort" explanation, apparent selectivity could conceivably be an artefact of error in estimating the relative abundance of each habitat type.

Biomass differences between habitat types: Utilisation of *A.etbaica* products (mainly flowers, but also pods, leaves, thorns and exudate) cannot explain why above-parity selection ratios for that species type were maintained throughout the year (see Table 3.10a), even in months when it made a negligible contribution to the diet. The possibility remains that general productivity of the habitat was greater than in the other two main species types.

Extraction of separate biomass estimates reveals that biomass of quadrats within *A.etbaica* habitat was higher than that of quadrats within *A.tortilis* habitat, but about the same as that of quadrats within *A.mellifera* habitat (means of monthly means: *A.etbaica*=3.518 g/m^2, *A.tortilis*=2.915 g/m^2, *A.mellifera*=3.359 g/m^2). Overall, the differences between the three sets of eight monthly means were not significant

($F=1.013$, $p>0.05$). Similarly, the differences between biomass estimates extracted separately for each density type were not significant ($F=0.887$, $p>0.05$).

These results suggest that average biomass differences between habitat types are insufficient to explain apparent selectivity. However, it must be cautioned that the means for each habitat type are in some cases derived from dubiously small samples; there were 10 points (20 quadrats) in *A.etbaica* habitat, and 11 points (22 quadrats) in *A.mellifera* habitat, but only 2 points (4 quadrats) within *A.tortilis* habitat. The same proviso applies to the separate estimates for density types, there being only 1 point (2 quadrats) in the case of open habitat. It may therefore be premature to conclude that habitats did not differ in their productivity.

Spatial associations between habitat types, sleeping sites and dams: Sleeping sites surrounded by *A.etbaica* habitat were used on 56% of known occasions, while the corresponding figures for sites surrounded by *A.mellifera* and *A.tortilis* are 10.9% and 20.2% respectively. Similarly, three of the four permanent dams used by the troop for drinking were located within *A.etbaica* habitat, the fourth being surrounded by *A.mellifera* woodland. Since foraging routes inevitably converge on and diverge out from these resources, it is possible that the preference for *A.etbaica* habitat is an incidental effect of this spatial association. With regard to tree density, three of the main sleeping sites (accounting for 78% of nights) were situated at the boundaries of light and thick bush zones, while the fourth was entirely surrounded by

light bush. Two of the four dams (the most frequently used ones) were surrounded by forest, the other two principally by thick bush. No sleeping sites or dams were close to open habitat.

It seems, then, that apparent preferences could have more to do with the geography of the home range than with inherent properties of the habitat types themselves. Against this it could be argued that the direction of causality goes the other way - that selection of particular sleeping sites and dams is contingent on their proximity to preferred habitats. The only way of resolving this is by examining the influences of each variable on differential range use while statistically controlling the influences of the other variables. This is the approach taken in the following section.

Multiple regression analysis of quadrat use: In order to evaluate the independent influences of (a) inherent properties of habitat types associated with species dominance and tree density, and (b) associations between habitat types and proximity to sleeping sites and dams, I have performed multiple regression analyses of quadrat use. Each 25 hectare quadrat in the home range (see Chapter 2) was scored for percent coverage of each of the three major species types, estimated by eye from the habitat map. As predicted by the selection ratios, the frequency of occupation of quadrats correlates positively with *A.etbaica* coverage (r=0.219, df=75 1-tailed p=0.049). However, the correlations with the other two species types are not significant (*A.mellifera*; r=0.089, p=0.255: *A.tortilis*; r=-0.049, p=0.361). Quadrats were also

scored for percent coverage by different density types, and these data were combined into single density indices for each quadrat, using arbitrary weightings in the formula:

$$DI = \frac{\%open+(\%light\ bush*2)+(\%thick\ bush*3)+(\%forest*4)}{400}$$

DI correlates positively with occupancy, as expected ($r=0.351$, 1-tailed $p=0.003$).

The second step in the analysis was to measure the distances from the centre of each quadrat to the nearest sleeping site and to the nearest dam (in millimetres on the ranging map). Using arcsine transformations of percentages, and then logarithmic transformation of all variables (to improve linearity), a stepwise multiple regression was performed on the pooled data for the whole study period, with quadrat occupancy as the dependent variable. Strictly, the independent variables in such an analysis should be statistically independent, because multicolinearities make valid estimation of beta weights and values of r^2 problematic (Marascuilo and Levin, 1983). However, in the SPSSX program used, candidate variables are evaluated for their "tolerance" (the amount of their variance not explained by the other independent variables in the regression equation) before qualifying for inclusion. If the tolerance of a variable exceeds the permitted level, a warning is printed. A solution at this stage is to perform principal component rotations on the variables to eliminate linear dependencies. However, this was not necessary in the present analysis because tolerance levels were not exceeded. The results, summarised in Table

3.8, indicate that, overall, the regression was significant, with about 60% of the variance in quadrat occupancy explained. Proximity to sleeping sites and to dams were significantly related to intensity of quadrat use, whereas neither the density index nor percent coverage by any of the three species types were.

Since the dependent variable was the total number of 15-minute point samples recorded for each quadrat, the significant influences of sleeping site and dam proximity could be due to more frequent use of quadrats, to longer stays in quadrats, or to both. Thus, although it has been established that the

TABLE 3.8: MULTIPLE REGRESSION ANALYSIS OF QUADRAT OCUPANCY

INDEPENDENT VARIABLE	BETA*	T	SIG T
Distance to sleeping site	-0.697	-6.340	<0.0001
Distance to dam	-0.367	-3.105	0.0001
A.etbaica coverage	0.085	0.771	0.4447
A.mellifera coverage	0.006	0.078	0.8862
A.tortilis coverage	-0.091	-0.121	0.7836
Density index	0.035	0.399	0.6915

$F=44.33$ $p<0.001$ Adjusted $r^2=0.603$

Notes: * Standardized regression coefficient

baboons' ranging patterns centred on sleeping sites and dams, there is still the question of whether this simply reflects the tendency for day ranges to converge on these essential resources or whether the areas around them were genuinely used more intensively by the baboons. If the latter is the case then quadrat bout length (the average duration of stays within a quadrat) should also be related to the distance measures.

In addition, analysis of quadrat bout length might reveal a relationship between differential range use and the habitat variables, concealed in the first analysis.

Another multiple regression was performed, this time with quadrat bout duration as the dependent variable (Table 3.9). The regression was significant, but only 7% of the variance was explained. The only variable which exerted a significant influence on the duration of stays within quadrats was distance to the nearest dam, indicating that the effect of sleeping site proximity found in the previous analysis was due

TABLE 3.9: MULTIPLE REGRESSION ANALYSIS OF MEAN QUADRAT BOUT DURATION

INDEPENDENT VARIABLE	BETA	T	SIG T
Distance to dam	-0.285	-2.225	0.030
Distance to sleeping site	-0.083	-0.634	0.529
A.etbaica coverage	-0.041	-0.249	0.805
A.mellifera coverage	0.013	0.180	0.912
A.tortilis coverage	-0.097	-0.256	0.788
Density index	0.058	0.437	0.664

F=4.949 p=0.030 Adjusted r^2 = 0.068

simply to the higher frequency with which quadrats near the convergence-divergence points of day ranges were entered.

In summary these analyses indicate that the discrepancies between observed and expected time-habitat budgets are best explained by the spatial associations between habitat type and sleeping sites and dams, rather than by inherent properties of the habitats themselves. However, the conclusion that habitat characteristics exerted no influence on the ranging of the

baboons would be premature for two reasons. Firstly, the admittedly rather crude methods of habitat classification and estimation of abundance within quadrats could be obscuring genuine relationships. In particular, explicit account was not taken of characteristics of the herb layer (though, as noted, these probably correlate to some extent with density and species dominance of trees and shrubs). Secondly, and perhaps more importantly, the effects of seasonal variation have not yet been taken into account; it is likely that any seasonally-dependent selectivity that existed would have been obscured by pooling data for the whole study period. This possibility is followed up in the next section.

(iv) Seasonal variation in habitat use and its determinants

Table 3.10 shows monthly variation in habitat use (time-habitat budgets and selection ratios) for the three major species types and for the collapsed density types. Also shown (in 3.10b) are values for the density selection index, which is analagous to the density index, and is calculated using percentage of time spent within each density category, according to the formula:

$$DSI = \frac{\%open+(\%light\ bush*2)+(\%thick\ bush*3)+(\%forest*4)}{400}$$

Species dominance: Month of observation was significantly associated with allocation of time to species types ($X^2=58.3$, df=14, $p<0.001$; data are one point per focal sample). As already noted, the selection ratio for

TABLE 3.10: MONTHLY VARIATION IN TIME-HABITAT BUDGETS AND HABITAT SELECTION RATIOS

(a) Major species types

	A.etbaica	A.mellifera	A.tortilis
MAY			
%	46.4	28.6	3.3
SR	1.78	0.88	0.15
JUNE			
%	35.6	24.4	8.5
SR	1.37	0.75	0.38
JULY			
%	40.3	30.8	12.4
SR	1.55	0.95	0.55
AUG			
%	36.6	26.0	5.4
SR	1.40	0.80	0.24
SEP			
%	64.4	15.4	3.9
SR	2.47	0.47	0.17
OCT			
%	33.6	19.5	26.4
SR	1.29	0.60	1.18
NOV			
%	52.3	25.2	3.2
SR	2.0	0.78	0.14
DEC			
%	33.8	37.8	12.6
SR	1.30	1.16	0.56

TABLE 3.10 cont.

(b) Density types

	2	3/8	4/7/9	5/6	DSI
MAY					
%	18.4	49.9	18.6	10.2	0.55
SR	2.76	0.97	0.56	4.34	
JUNE					
%	5.2	47.0	31.3	3.7	0.59
SR	0.78	0.91	0.95	1.57	
JULY					
%	2.1	47.2	34.5	8.7	0.63
SR	0.31	0.92	1.04	3.70	
AUG					
%	1.0	50.3	17.8	7.1	0.60
SR	0.15	0.98	0.54	3.02	
SEP					
%	0.1	37.3	33.3	11.3	0.67
SR	0.01	0.72	1.01	4.81	
OCT					
%	1.6	42.1	36.7	4.9	0.64
SR	0.24	0.82	1.11	2.08	
NOV					
%	3.6	25.3	47.9	8.4	0.68
SR	0.54	0.49	1.45	3.57	
DEC					
%	6.3	56.6	23.2	2.0	0.56
SR	0.94	1.10	0.70	0.85	

Notes: % = % of point samples SR = selection ratio DSI = Density selection index

A.etbaica habitat was maintained above parity throughout the study period, while ratios for *A.mellifera* and *A.tortilis* were below parity for seven out of eight months in both cases.

The proportion of time spent in each species type is significantly or near-significantly correlated with the proportion of feeding time devoted to that species (*A.etbaica*; r=0.675, p=0.033: *A.mellifera*; r=0.733, p=0.019: *A.tortilis*; r=0.594, p=0.054: n=8 in each case). Thus diet and differential habitat use do appear to be linked. This association could be a side-effect of some independent factor influencing ranging; whatever caused the troop to be in a particular area at a particular time, diet would be constrained by what was available there. That this is not the case (i.e. that the baboons actively selected habitat types on the basis of food availability) is strongly suggested by the fact that the proportion of time spent in each species type is also significantly correlated with productivity (g/m^2 dry weight of food) of the given species (*A.etbaica*; r=0.658, p=0.041: *A.mellifera*; r=0.870, p=0.008: *A.tortilis*; r=0.876, p=0.006: n=8).

Despite any differences that might exist in the structure and composition of the herb layer in species types, there were no significant correlations between the proportion of time spent in the latter and average herb layer biomass (*A.etbaica*; r=-0.429, p=0.145: *A.mellifera*, r=0.469, p=0.120: *A.tortilis*, r=-0.072, p=0.433: n=8).

Tree/shrub density: Month of observation was also significantly associated with allocation of time amongst density types (X^2=87.6, df=21, p<0.001). Once again, however, a potential problem is that species dominance and density may be confounded; the DSI is near-significantly correlated with the percentage of time spent in *A.etbaica* habitat (r=0.584, df=6, p=0.097) and in *A.mellifera* habitat (r=⁻0.639, df=6, p=0.064), though not with time in *A.tortilis* habitat (r=⁻0.036, df=6, p=0.616). Thus, increases in time spent in more densely wooded areas might simply reflect increases in preference for *A.etbaica* habitat, and *vice versa*. However, if similar trends of monthly variation in occupancy of the different species types exist *within* density types, it would be valid to conclude that density has some independent influence on ranging. This possibility was examined by testing for concordance of monthly variation within density types: monthly allocation of time to density types was significantly concordant across species types for open areas (w=0.6687, x^2=14.482, p=0.047), but not for light bush (w=0.5027, x^2=10.556, p=0.159), thick bush (w=0.3348, x^2=9.376, p=0.227) or forest (w=0.4162, x^2=5.826, p=0.560). Thus it seems that there is variation in use of open areas independent of variation in selection for species type, but that variation in other density types is largely or entirely linked to species type selection. This makes it difficult to interpret seasonal variation in habitat use, but the correlations between time spent in species types and the productivity and intensity of utilisation of these species suggests that species dominance *per se* is an important factor.

What other evidence is there that density has independent influences on ranging? There is a significant negative correlation between DSI and biomass of herb layer foods ($r=^{-}0.699$, df=6, p=0.042), but no correlation between DSI and biomass of tree foods (r=0.306, df=6, p=0.460), implying that the baboons spent more of their time in relatively open habitats when herb layer productivity was high. When the effect of tree food biomass is controlled, the correlation between DSI and herb layer food biomass remains significant (partial $r=^{-}0.672$, df=5, p=0.050). Conversely, the correlation between DSI and tree food biomass remains non-significant when the effect of herb layer food biomass is controlled (partial r=0.212, df=5, p=0.324).

To control for the effect of variation in species type utilisation, these analyses were repeated individually for the three main species types. The matrix of correlations is presented in Table 3.11.

TABLE 3.11: PEARSON AND PARTIAL CORRELATIONS BETWEEN DENSITY SELECTION INDEX AND BIOMASS OF FOODS IN HERB LAYER AND IN TREES

SPECIES TYPE	PEARSON r		PARTIAL r	
	HLB	TB	HLB_{TB}	TB_{HLB}
A.etbaica	$^{-}0.741^{*}$	0.290	$^{-}0.724^{*}$	0.185
A.mellifera	$^{-}0.336$	$^{-}0.164$	$^{-}0.349$	$^{-}0.101$
A.tortilis	0.600°	0.041	0.626°	0.228

HLB = Herb layer food biomass TB = Tree food biomass

* $p<0.05$ $^{\circ}$ $p<0.07$

The results indicate an interaction between the influences of species dominance and tree density, in terms of responses to herb layer biomass fluctuations: the expected negative correlation between herb layer biomass and DSI is found within *A.etbaica* habitat, but is not significant within *A.mellifera* habitat. In contrast, within *A.tortilis* habitat, there is a near-significant *positive* correlation between DSI and herb layer food biomass. These patterns remain when the effects of tree food biomass are partialled out.

Multiple regression analysis of quadrat use in four seasons: At the end of section (iii) it was noted that the conclusion that habitat composition of quadrats did not influence the intensity of their utilisation by the baboons was premature because seasonality had not been taken into account. Subsequently it was shown that the amount of time spent in particular habitats varied significantly across months, and, in the case of species types, correlated with the productivity and intensity of use of the relevant species. In this section the theme of seasonal variation in differential range use is pursued by examining quadrat occupancy separately for two wet seasons (April-July and November/December) and two dry seasons (January-March and August-October). The main question concerns whether or not there are seasonally-dependent influences on quadrat utilisation that were obscured in the analysis of pooled data.

Stepwise multiple regressions were performed on the four data sets, with total, rather than average, quadrat occupancy as

the dependent variable (data were too sparse to permit use of the latter). The results are presented in Table 3.12. Regressions were significant in each case, with between 37% and 68% of the variance explained. The results reflect those for the pooled data (Table 3.8) in that distance to sleeping sites and dams were significant influences on quadrat occupancy in all four seasons. In addition, tree density (as measured by the TDI) was a significant positive influence in the first dry season, as was percent *A.etbaica* coverage in the second dry season. None of the habitat variables were significant influences in either wet season.

Splitting the analysis of quadrat use in this way has revealed some seasonally-dependent selectivity in habitat use obscured in the analysis of pooled data. Thus, evidence has been obtained that habitat composition does have some influence on ranging, independently of the spatial associations between habitat type and sleeping sites and dams. Specifically, the idea that more densely-wooded habitats are preferred when herb layer biomass is low has received limited support. The positive association between quadrat use and *A.etbaica* coverage in the second dry season reflects the intensive utilisation of the species as a food source at that time. Perhaps surprisingly, the influence of distance to the nearest dam persisted in the two wet seasons, despite the wider availability of water.

While habitat composition had no discernible influence on quadrat use in the two wet seasons, this should not be taken as definitive evidence for there being no habitat preferences

TABLE 3.12: MULTIPLE REGRESSION ANALYSES OF TOTAL QUADRAT OCCUPANCY IN FOUR SEASONS

DRY 1

INDEPENDENT VARIABLE	BETA*	T	SIG T
Distance to sleeping site	-0.420	-3.433	0.0011
Tree density index	0.408	3.314	0.0016
Distance to dam	-0.327	-2.164	0.0132

$F = 10.573$ $p<0.001$ adjusted $r^2 = 0.351$

Variables not in the equation: *A.etbaica, A.mellifera, A.tortilis* coverage.

DRY 2

INDEPENDENT VARIABLE	BETA*	T	SIG T
Distance to sleeping site	-0.627	-7.195	<0.0001
Distance to dam	-0.355	-4.082	0.0001
A.etbaica coverage	0.204	2.132	0.0021

$F = 40.411$ $p<0.001$ adjusted $r^2 = 0.680$

Variables not in the equation: *A.mellifera, A.tortilis* coverage, tree density index.

WET 1

INDEPENDENT VARIABLE	BETA*	T	SIG T
Distance to sleeping site	-0.579	-5.749	<0.0001
Distance to dam	-0.266	-2.639	0.0108

$F = 23.280$ $p<0.001$ adjusted $r^2 = 0.439$

Variables not in the equation: *A.etbaica, A.mellifera, A.tortilis* coverage, tree density index.

WET 2

INDEPENDENT VARIABLE	BETA*	T	SIG T
Distance to sleeping site	-0.545	-5.123	<0.0001
Distance to dam	-0.237	-2.226	0.0302

$F = 18.070$ $p<0.0001$ adjusted $r^2 = 0.375$

Variables not in the equation: *A.etbaica, A.mellifera, A.tortilis* coverage, tree density index.

Notes: * standardised regression coefficient

at all at that time. It is important to stress again the somewhat crude methods of habitat classification and quantification within quadrats; a more fine-grained approach, beyond the scope of this project, might have enabled the identification of further relevant parameters influencing differential range use by the baboons. Given this, the significant effects found within the two dry seasons are encouraging and provide a basis for future work.

(v) Discussion of differential range use

The baboons use of space was evidently not random; ranging patterns were centred on sleeping sites and dams throughout the year, and there were seasonal changes in preferences for particular habitat types related to changes in food availability.

The influence of sleeping site proximity on total quadrat occupancy is unsurprising, given that ranging routes must inevitably converge on and diverge out from these points, and when the *average* duration of stays was considered, no effect was apparent.

In contrast, proximity of dams did influence average quadrat bout duration, as well as total utilisation. It is, of course, very difficult to entirely separate the effects of water proximity and vegetation by statistical means, because they are, to an extent, *inherently* associated with one another; that is, the presence of water will inevitably influence the composition of the local vegetation. I have

only quantified the abundance of gross habitat types, which ignores the possible effects of subtle vegetational differences. However, the presence of subterranean water along the network of dry wadis, which covered the whole home range, apparently had a very similar influence on vegetation, so that the effects of vegetation and of drinking water are, to a degree, separable. Furthermore, the baboons did not particularly concentrate their feeding activities in the *immediate* vicinity of the dams (i.e. within the few metres directly affected by the presence of the water). They did, on the other hand, regularly come to dams to drink. It seems, therefore, quite safe to conclude that the need for drinking water *per se* influenced the ranging patterns of the troop.

This fits with qualitative observations that water availability determines both what areas baboons can survive in, and where they go within their home range (Altmann, 1974; Sharman,1981 refs.). Lindburg (1977) came to a similar conclusion in his study of rhesus monkeys (*Macaca mulatta*) inhabiting dry woodland in India. To my knowledge, the results reported here are the first quantitative demonstration of a relationship between water distribution and differential range use. Since the actual process of drinking enough to satisfy requirements takes up relatively little time, the relationship is probably largely a consequence of baboons preferring to forage in areas conveniently close to water sources, rather than directly related to use of the resource itself. Water has a more restricted distribution in the dry season, and this may have contributed to the corresponding increase in day range lengths found in the present study.

The importance of water for baboons is probably due in part to the thermoregulatory requirements of life in savannahs. While moving about in the open during the middle of the day, animals are exposed to intense insolation and radiation of heat from the ground (any fieldworker will testify to this!). Baboons maintain core temperatures by sweating and panting (Funkhouser *et al.*, 1967), both of which involve evaporation of water. Hiley (1976) found that cutaneous water loss in captive baboons subjected to heat exposure at 40^{o}C increased by about 360%. Behavioural thermoregulation has the advantage that water loss is not incurred, and several workers have reported that baboons rest in the shade during the hottest part of the day (Altmann and Altmann, 1970; Stolz and Saymann, 1970). It would be interesting to see whether the extent to which this strategy is used in different populations is related to water availability.

Use of shade as a form of behavioural thermoregulation could have implications for differential range use, if certain areas provide better cover than others. I do not have the data to answer this, but the question has been addressed by Stelzner (1988) in one of the few published multivariate analyses of range use in primates. Using general linear modelling of quadrat choice in relation to shade availability and heat load, controlling for time of day, Stelzner found that intensity of quadrat use by yellow baboons (*Papio cynocephalus*) in Amboseli National Park was unrelated to the shade-giving characteristics of the vegetation. Instead, animals used shade opportunistically by slowing rates of

travel and spending more time resting when they encountered shaded areas.

Sharman (1981) reported that availability of shade influenced the frequency with which quadrats were entered by troops of Guinea baboons (*Papio papio*). As in the present study, he also found that differential home range use was related to sleeping site proximity, and also to topography, visibility, and habitat type. However, these results are difficult to interpret because no attempt was made to evaluate the independent contributions of each variable with the effects of the other variables statistically controlled. It seems particularly likely, for example, that shade availability and visibility were confounded, and the same goes for topography and habitat type.

The use of multiple regression analysis here has revealed the importance of statistical control of confounding variables in the analysis of differential range use. Had only the habitat selection ratios or the bivariate correlations between quadrat use and habitat composition been considered, for example, this would have led to the erroneous conclusion that there was an overall preference for *A.etbaica* habitat, and perhaps, given enough deliberation and imagination, it would have been possible to concoct a spurious explanation based on some inherent property of the habitat. As mentioned above, there have been few attempts of any kind to control confounding variables in studies of range use in primates; indeed, many studies have resorted to mere qualitative evaluation of

bivariate relationships between ranging and resource distribution.

Two other studies, both on baboons, have been carried out, in which some attempt was made to evaluate the independent influences of more than one habitat variable on differential range use. Sigg and Stolba (1981) controlled for distance from the sleeping site by comparing the frequency of use of quadrats assigned to one of three habitat types within four concentric distance rings. Using this procedure, it was found that wadis were preferred to high plains. Sigg and Stolba argued that the reason for this preference was the lower risk of finding no food in wadis. In another study, Post (1978) used multiple regression to investigate the influence of habitat composition on quadrat use in yellow baboons (*Papio cynocephalus*). Similarly to the analyses presented here, overall frequency of use of quadrats was regressed on percentage cover values for the different habitat types. The overall regression was significant, although the coefficients for particular habitat types did not correlate well with measures of habitat value. The influence of sleeping site and waterhole proximity were not evaluated in the regression; instead, Post examined the residuals for quadrats containing these features, finding a significant effect of presence of sleeping sites but not of waterholes (though the non-significant effect was in the predicted direction). The latter may seem surprising given the results obtained in the present study. However, the procedure used by Post is likely to be relatively insensitive, since only effects on the actual quadrat containing the waterholes were considered.

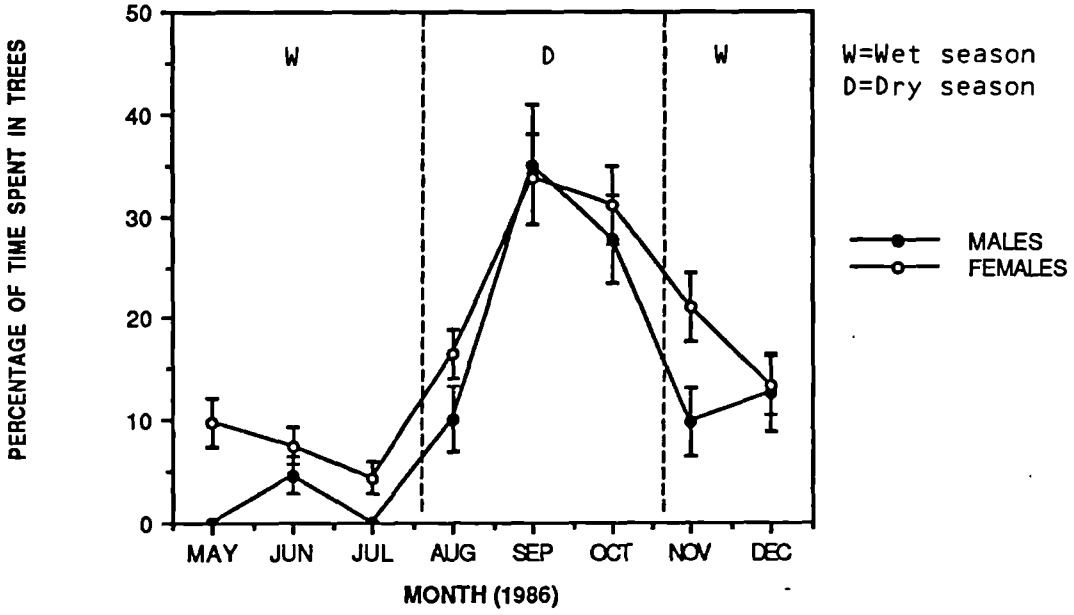
(f) Arboreality

Focal animals (therefore not juveniles) spent a mean of 9.69% of their active day off the ground in trees (mean of monthly means). This is less than the 14.5% figure for Sharman's (1981) *Papio papio* study population (calculated from his data as %feeding records in trees multiplied by proportion of time spent feeding), probably a reflection of the fact that Sharman's Senegal study site was relatively thickly wooded. Dunbar and Dunbar (1974) reported that 27.9% of their sightings of *Papio anubis* at a study site in Ethiopia were animals in trees, but this may overestimate the amount of time spent in trees, since it is likely that such animals are more visible than those on the ground.

Monthly variation in the mean percentage of time spent in trees is negatively correlated with herb layer biomass ($r=^{-}0.745$, df=6, p=0.034), but, perhaps surprisingly, the correlation with tree food biomass, though in the expected direction, is not significant (r=0.508, df=6, p=0.200). The correlation with herb layer food biomass remains significant when the effect of tree food biomass is held constant (partial $r=^{-}0.750$, df=5, p=0.048). The correlation with tree food biomass remains non-significant when the effect of herb layer food biomass is held constant (partial r=0.520, df=5, p=0.232). Thus the baboons' arboreality seems to have been most strongly affected by the availability of terrestrial foods.

The percentage of time spent in trees in each month is shown separately for males and females in Figure 3.11. Females spent more time in trees than did males, except in September, and the difference is significant (paired $t=-3.11$; $df=7$, $p=0.017$). There are at least three possible explanations for this difference in arboreality. Firstly, male baboons are nearly twice the weight of females, and the relative energetic cost of climbing increases with body size (Peters, 1983). Secondly, males' greater weight will inevitably limit their ability to climb about on terminal branches and twigs. Thirdly, an alternative way in which trees were exploited by the baboons was by plucking food items from branches pulled down and held onto from a position on the ground; males' greater strength and weight must have made this easier. The tendency for larger individuals to spend less time feeding in terminal branches, or more time feeding on the ground, has been observed in a number of species, including *Papio hamadryas, Cercocebus albigena, Colobus badius, Symphalangus syndactylus, and Gorilla g. berengei* (reviewed by Clutton-Brock, 1977, pp. 544-545). As we shall see, however, this difference iss not necessarily associated with dietary divergence (Chapters 5 and 6).

FIGURE 3.11: PERCENTAGE OF TIME SPENT IN TREES BY MALES AND FEMALES



CHAPTER 4: FEMALE DOMINANCE RELATIONS, REPRODUCTIVE PROFILES, AND BODY CONDITION

1. INTRODUCTION

This chapter lays the groundwork for the analyses of female ecological and social strategies developed in the succeeding chapters. The particular interest in females derives from two related sources. Firstly, female mammals are confronted by considerable physiological costs associated with gestation and especially lactation (Payne and Wheeler, 1968; Hanwell and Peaker, 1977; Sadleir, 1973), and how these translate into constraints on diet, energy intake and time-budgeting is of central importance in understanding the relationship between ecology and patterns of reproductive investment (e.g. Altmann, 1980; Lee, 1987; Dunbar and Dunbar, 1988). Secondly, because of these costs, female reproductive success is probably constrained importantly by nutritional status, and thus by foraging efficiency; social structure is therefore expected to be intimately linked to female foraging stategies and patterns of dispersion (Bradbury and Vehrencamp, 1977; Emlen and Oring, 1977; Wrangham, 1979, 1980; Greenwood, 1980; Wittenberger, 1980; Ims, 1988). In this chapter I provide a basic description of social relationships among females, and examine trends in their reproductive investment and body condition.

In most cercopithecine monkeys, females form the core of society, invariably remaining in their natal troop to breed, and forming well-differentiated, stable, long-term

relationships with one another, in which agonistic dominance is an important component (e.g. Kawai, 1958; Wrangham, 1980; Hausfater *et al.*,1982; Sade, 1972a; Cheney *et al.* 1981; Chism and Rowell, 1986; but c.f. Moore, 1984). Richard Wrangham has argued that this type of social organisation is associated with a particular set of ecological conditions promoting intraspecific feeding competition (Wrangham, 1980). The gist of this model is that "female-bonded" groups evolve in response to a particular pattern of food distribution; if food occurs in relatively high-quality, defendable patches, at least during part of the year, it may be worthwhile for individuals to form permanent alliances in order to gain exclusive access to those patches when they are encountered. However, the cost of enhanced access to patches is competition within the group (Wrangham, *op cit.* pp.267 and 283), and whenever feeding sites are limited in number or variable in quality, competitive exclusion will result in certain individuals doing better than others. It is argued that so-called *dyadic dominance*, which may actually be dependent on alliances formed with other group members (Cheney, 1977; Walters, 1980; Datta, 1983; Berman, 1983; Harcourt and Stewart, 1987), will influence individuals' foraging success, in a way which parallels the effects of *intergroup dominance*. The twin needs to cooperate against other groups, and to compete within the group, are seen as the driving forces behind the development of highly differentiated relationships among females. Wrangham's claim, therefore, is that the model explains both the evolution of group-living and the internal structure of the groups so formed.

The model has been criticised on the basis that it discounts an important role for predation pressure in the evolution of group-living (van Schaik, 1983, 1989; Dunbar, 1988). Wrangham has argued that the ability of his model to account for both the *occurrence* and the *form* of group life makes it preferable to a predation model, which only accounts for the former (though see van Schaik, 1989). The reason for this view is not entirely clear; as noted in Chapter 1, whatever the ecological pressures responsible for the evolution of groups, it seems perfectly plausible that female-bonding and male dispersal could have been secondary responses to this. The theory that female-bonding is functionally related to feeding competition does not depend on group-living *per se* having evolved for the same reason.

These considerations suggest that the issue of group-living, and the issue of groups' internal organisation, can be decoupled. Evaluation of models of the evolution of groups is outside the scope of the present project, but the functional significance of female social relationships within groups is a central concern of it. In particular, I shall focus on the behavioural and nutritional implications of dominance, an approach taken by a number of previous researchers (Dittus, 1979; Jones, 1980; Post *et al.*, 1980; Wrangham, 1981; Wrangham and Waterman, 1982; Whitten, 1983; van Noordwijk and van Schaik, 1987; Janson, 1988). The concept of dominance amongst primates is, however, not uncontroversial (Gartlan, 1968; Rowell, 1974; Altmann, 1981; Strum, 1982; see Dunbar, 1988 pp.206-208, for a summary), and it is not valid to simply assume that a linear hierarchy exists if this has not been

tested. There may be considerable ecologically- and demographically-related variation in the importance and structure of intragroup competition, both within and between species (Chapais and Schulman, 1980; Datta, 1988; van Schaik, 1989). Consequently, the nature and distribution of affiliative behaviours are also likely to vary. Part of this chapter is therefore concerned with examining patterns of dominance and affiliation within the cohort of 26 adult females in the study group, and in particular with the question of whether a linear hierarchy best accounts for the observed distribution of interactions.

The oestrous cycles and reproductive behaviour of *Papio* baboons have been described before (Rowell, 1969; Hendrikx and Kraemer, 1969; Saayman, 1971a; Scott, 1984), and it is not my intention to analyse these phenomena in detail. However, basic data on the timing of reproduction during the study year will be presented, and related to ecological constraints (bearing in mind the severe limitations of a short study), and to body condition.

2) SOCIAL ORGANISATION AMONGST FEMALES

The following sections provide a basic description of the dominance structure and patterning of agonistic and affiliative interactions amongst the adult females. Both *ad libitum* observations on all 26 adult females and focal data on the subset of 19 sampled females are used. The scope of the analysis is fairly modest, concentrating on the essential

features relevant to competition. Because of this, I am probably only scratching the surface of the social complexity (for more comprehensive analyses of the dynamics and determinants of social relationships in baboons, macaques and other species, see Hinde, 1983b).

(a) Female dominance hierarchy

The following analysis utilises 532 observations of dyadic agonistic interactions between adult females. These comprise 361 *ad libitum* observations, and 171 observations extracted from focal samples. Excepting supplants over food, all types of agonistic and approach/avoid interactions (see Chapter 2) were pooled and scored according to winner and loser (food supplants are analysed separately in Chapter 7). Using these data it was possible to determine the direction of dominance for 212 of the 325 dyads (65%). Appleby (1983) presents a method for evaluating the linearity of hierarchies, based on the estimated number of circular triads. Using this procedure it is found that a significantly linear hierarchy existed among the STT females ($d=442.75$, $x^2=107.77$, $df=32.2$, $p<0.001$). The coefficient of linearity is only $K=0.392$, lower than any of those presented for four study groups of savannah baboons in the review by Jackson and Winnegrad (1988). However, this cannot be taken as evidence for relatively low linearity in the STT cohort, because the value of K is inversely related to the proportion of undetermined dyads; in the present study this was 34.7%, whereas Jackson and Winnegrad excluded data sets having more than 20% of dyads undetermined.

The significant result obtained permits the construction of a linear dominance hierarchy, with individuals arranged so as to minimise the number of circular triads. When this is done (Figure 4.1), 17 of the observed interactions, or 3.2%, are reversals "against" the hierarchy. Of these 17, 12 were between individuals no more than three ranks apart, and 5 were between adjacently ranked individuals. Fifteen of these reversals occurred between animals in the bottom half of the hierarchy, suggesting that dominance relations may have been more stable in the top half. In two relationships, dominance runs counter to the hierarchy. One of these (LE and KH) is based on only one interaction. The other is between ET and HO, who were only 3 ranks apart.

Although I did not try to evaluate dominance relations during the course of the fieldwork, it is probably inevitable that subjective impressions will be formed by simple virtue of making the observations. Because it is conceivable that initial impressions bias subsequent observations towards reinforcement of putative dominance relations, I have performed an inter-observer reliability test. A high correlation exists between the hierarchy in Figure 4.1 and that constructed from an entirely independent data set by D.Lochhead, from her 1987 study (r_s=0.983, df=24, $p<0.001$). I did not discuss my subjective impressions with Lochhead, nor show her my results until the conclusion of her fieldwork. This both validates the hierarchy, and indicates some stability between years. The only differences between the two hierarchies were found amongst the bottom ten positions, which is perhaps further evidence for less stability than amongst

	EU	MA	PR	TR	KH	DI	AT	CT	MR	SH	GR	ML	C1	FT	NI	LE	OP	TK	ET	TW	CH	HO	BI	LA	EL	AQ
EU*	--	5	3	2	1	2	5	3		5	3	3	1	3	3	1		2	1	1	5		2	2	3	3
MA*		--	2	1	3	1	2		1	1	2	1		5			1		1	1	4		1	1		1
PR*			--		1	1	5										1	1	3	1		1	1		2	
TR				--	1	5	4			1	1	1				1	1	2					1		2	
KH					--	2	6		1	1	3	3	1				2	1		1		1	1	1		
DI*						--	6	3	1	2	1			2	2		1			4	1	2	3			
AT*							--	1	1		2	4	1	7	4	2	2	1		2	4	1	1		1	
CT								--	1	1							1		1			1				
MR									--	1	1				1	3			1	3	4		3	1	1	1
SH*									1	--	7	8		4	1			1		2	6				2	
GR*										1	--	7	2	2	1			4	1							
ML*									1			--	1	4	4	2	3	1	3	2		2	3		1	
C1													--	2	2	5					1				3	
FT*														--	2	5	3		5	5	1	1	1		4	
NI*															--	3	4	1	2	6	4		2	1	3	2
LE*					1					1						--	3	2	7	2	1		5	1	4	2
OP*					1												--	1	1	2	11	2	3		8	
TK																1		--	1	2	2		1		3	1
ET*												1							--	2		1		1	2	4
TW*																			1	--	7	2	1		5	1
CH*																1				1	--	1	1	4	4	
HO*										1									4			--	1	3	1	
BI*																					1		--	2		2
LA*																							1	--	1	1
EL*																									--	3
AQ																										--

* Focal animals

FIGURE 4.1: DISTRIBUTION OF AGONISTIC INTERACTIONS (ADULT FEMALES)

Numbers are totals of observed agonistic interactions for each dyad, with individual on vertical axis scored as winner. Combined focal and ad lib. data, excluding feeding supplants

the higher positions. When the troop split in 1987, the division separated the bottom third of the hierarchy fairly neatly from the top two-thirds (Lochhead, *pers. comm.*).

(b) Distribution of agonistic and affiliative interactions among females

In this section I examine the broad distribution patterns of social interactions in relation to dominance and the magnitude of differences in rank between dyad members. To a certain extent this discussion is tangential to the main thrust of the study, in that it does not bear directly on the issue of resource competition. It is, however, justifiable on the following count. Knowledge of the distribution patterns of social interactions may be helpful in eventually coming to understand the *polyadic* nature of resource competition. Thus, since competition generates cooperation between individuals (e.g. Hall and DeVore, 1965; Alexander, 1974; Packer, 1977; Cheney, 1977; Wrangham, 1980; Dunbar, 1984a, 1988), establishing with whom individuals compete and with whom they cooperate will ultimately be an important element in understanding the way that competitive processes operate within groups.

In the female-bonded primates studied to date, it has been found that, because mothers assist daughters in acquiring ranks similar to their own, kinship and rank differences are confounded (**Macaques**: Kawai, 1958; Sade, 1965; Missakian, 1972. **Vervets**: Horrocks and Hunte, 1983. **Baboons**: Cheney, 1977; Walters, 1980). The genetic relatedness of adult

females in the present study is not known, but there is no reason to suspect that STT are any different from other groups, and this must be borne in mind in interpreting the following findings.

Also examined below are the influences of reproductive state on the various interaction rates. There were generally insufficient data to compare state-specific rates for individual months. Therefore, the approach taken is to examine relationships between reproductive profiles of different females during the whole study period, and their overall rates of interaction. The variables used are the percentage of months spent cycling, and whether or not females had a black infant for at least three months during the study period (both sexual receptivity and the presence of young infants have been shown to influence interaction rates among females in previous studies (Seyfarth, 1976; Wasser, 1983; Dunbar, 1978). Since the percentage of months spent cycling was uncorrelated with dominance rank (r_s=0.062, df=16, p=0.806), and since, of the three females with black infants during the main study period, one was high-ranking, one middle ranking and one low-ranking, it is unlikely that any observed effects of rank or reproductive state will be due simply to the confounding influence of the other. However, because relationships with these variables could obscure one another, I have calculated Kendall partial rank correlation coefficients, controlling for rank and percentage of months cycling alternately (Table 4.1). Unfortunately, the sampling distribution of this statistic is not known (Siegel, 1956), so the results only give a rough indication of the change in the

degree of correlation when the effects of one variable are held constant (like Kendall's tau, coefficients range from +1 to -1).

The analyses of interaction rates presented below are based on the focal sample data, with sample sizes as follows: agonistic n=171 interactions; affiliative approach n=160 interactions; grooming n=90 bouts; 18 adult females - DI excluded due to insufficient data. I concentrate on the effects of dominance rank on overall rates of interaction, and on the influence on interaction rates of the difference in rank between members of dyads. In the case of the latter I have permitted a minimum sample size of 5 dyads for calculation of mean interaction rates, giving an overall sample size for correlations of 21 (since the total number of adult females in the cohort was 26).

(i) Agonistic interactions: Not surprisingly, high-ranking females (HRFs) received aggression from or avoided other females at lower rates than did low-ranking females (LRFs) ($r_s=^-0.659$, one-tailed $p=0.003$), and HRFs were aggressive towards or avoided by other females more frequently than were LRFs ($r_s=0.765$, $p<0.001$). However, rank was not significantly related to the overall rates at which individuals participated in these interactions with other females ($r_s=^-0.335$, $p=0.174$).

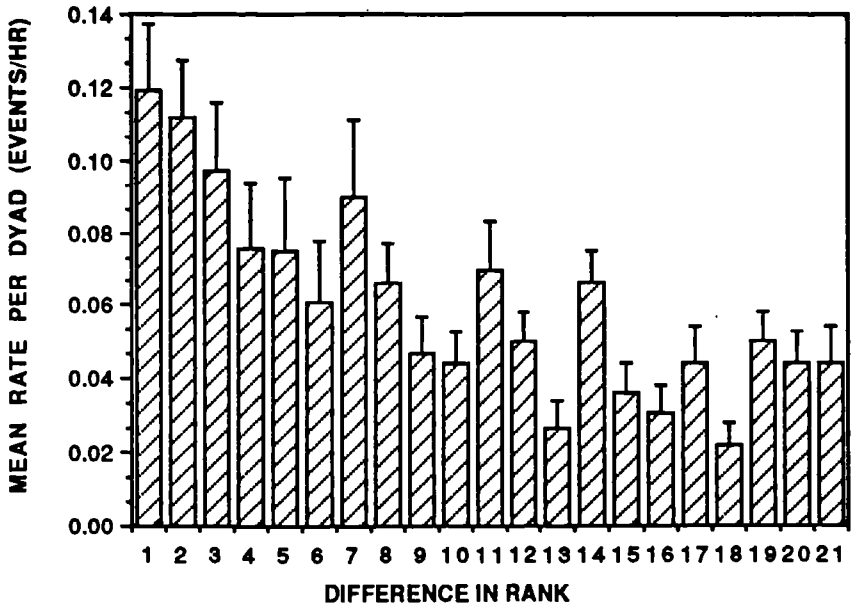
The magnitude of the difference in ranks between the members of a dyad strongly influenced the frequency with which they engaged in agonistic interactions ($r_s=^-0.835$, $p<0.001$). Thus,

most agonism occurred between adjacently-ranked individuals (Figure 4.2).

With respect to the reproductive profiles of focal females, there were no significant associations between the percentage of months spent cycling during the study period and the rate of receipt of aggression from other females (rate of receiving aggression/avoiding; r_s=0.163, p=0.517: rate of directing aggression at others/being avoided; r_s=⁻0.025, p=0.922: total rate of agonistic encounters with other females; r_s=0.017, p=0.948). Nor does the strength of these associations change much when the effect of rank is partialled out (Table 4.1). Females that had black infants during part of the study period directed aggression at or were avoided by others at a higher rate than those that did not (t=⁻2.34, df=16, p=0.032), but the two groups did not differ in the rate at which they received aggression from or avoided other females (t=0.82, df=16, p=0.424), nor in the total rate of aggressive encounters (t=⁻1.84, df=16, p=0.084).

Adult males were more frequently aggressors of or avoided by adult females than were other adult females (n=70 and 54 interactions respectively). These frequencies depart significantly from those expected on the basis of the number of potential interactees of each sex present in the group (X^2= 10.61, df=1, p<0.01). Breaking this down further, there was no difference in the frequencies with which focal females received aggression from adult males and from other adult females (48 interactions in each case; X^2=2.53, df=1, p>0.10,

FIGURE 4.2: RELATIONSHIP BETWEEN RANK DIFFERENCE AND RATE OF AGONISTIC INTERACTIONS *



* Rates determined from focal samples

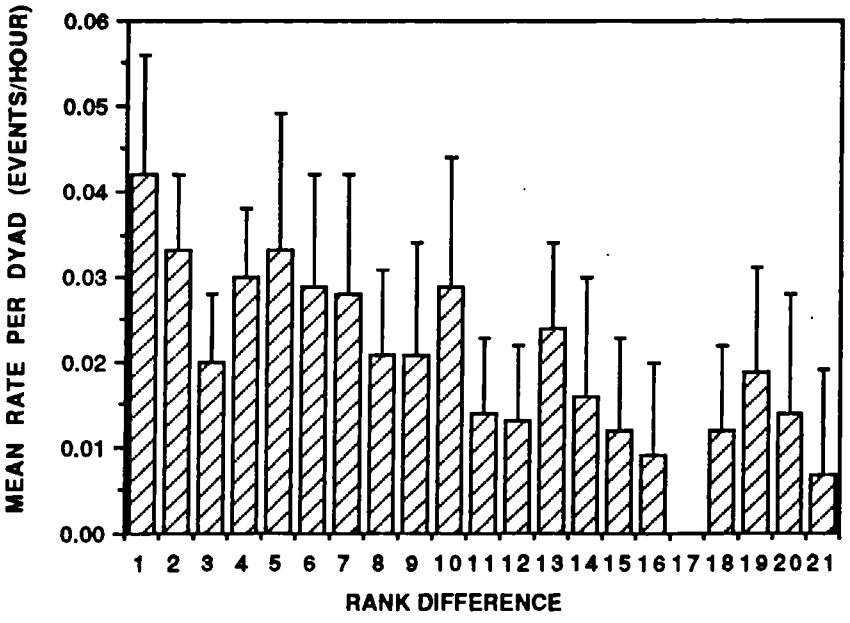
with expected frequencies according to numbers of males and females present).

However, with the limited data available, it appears that focal females more frequently avoided males than they did other females (22 versus 6, $X^2=15.62$, df=1, $p<0.001$ - the low overall rates of these subtle interactions are probably attributable to the observation methods, which involved close visual scrutiny of feeding). The frequency with which females received aggression from males was unrelated to either rank ($r_s=^-0.137$, p=0.653) or percentage of months cycling ($r_s=^-0.269$, p=0.332; see also Table 4.1).

(ii) Affiliative approaches: Dominance rank was not significantly associated with the frequency with which focal females received affiliative approaches from other females ($r_s=0.073$, p=0.773), the frequency with which they made such approaches ($r_s=^-0.257$, p=0.303), or the total frequency of approaching and being approached ($r_s=^-0.042$, p=0.868). The lack of associations appears to remain when the effect of percentage of months cycling is partialled out (Table 4.1). Nor was there an appreciable difference in the frequencies with which affiliative approaches were made "up" the hiearchy rather than down it (54% and 46% respectively, $X^2=2.24$, df=1, $p>0.10$).

As with agonistic interactions, the difference in rank between members of dyads strongly influenced the rate at which affiliative approaches were made, closely ranked females approaching one another more frequently than distantly ranked females ($r_s=^-0.824$, $p<0.001$ - see Figure 4.3).

FIGURE 4.3: RELATIONSHIP BETWEEN RANK DIFFERENCE AND RATE OF AFFILIATIVE APPROACHES*



* Rates determined from focal samples

TABLE 4.1: MATRIX OF KENDALL CORRELATIONS AND PARTIAL CORRELATIONS BETWEEN INTERFEMALE INTERACTION RATES, DOMINANCE RANK, AND PERCENTAGE OF MONTHS CYCLING

Interaction	Rank	$Rank_{MC}$[1]	Cycles	$Cycles_R$[2]
Agonistic				
a) Recipient	$^{-}0.543^{**}$	$^{-}0.546$	0.109	0.147
b) Actor	0.621^{**}	0.622	$^{-}0.014$	0.005
c) Total	0.216	0.215	$^{-}0.027$	0.023
Approaches				
a) Recipient	0.020	0.039	$^{-}0.624^{**}$	$^{-}0.624$
b) Actor	$^{-}0.203$	$^{-}0.202$	0.068	0.064
c) Total	$^{-}0.021$	$^{-}0.011$	$^{-}0.366^{*}$	0.367
Grooming				
a) Recipient	0.119	0.120	$^{-}0.473^{**}$	$^{-}0.474$
b) Actor	$^{-}0.046$	$^{-}0.043$	0.149	0.148
c) Total	$^{-}0.059$	$^{-}0.071$	$^{-}0.312$	$^{-}0.314$

** $p<0.001$ * $p<0.05$

[1] Correlation with rank, percentage of months cycling partialled out.
[2] Correlation with percentage of months cycling, rank partialled out.

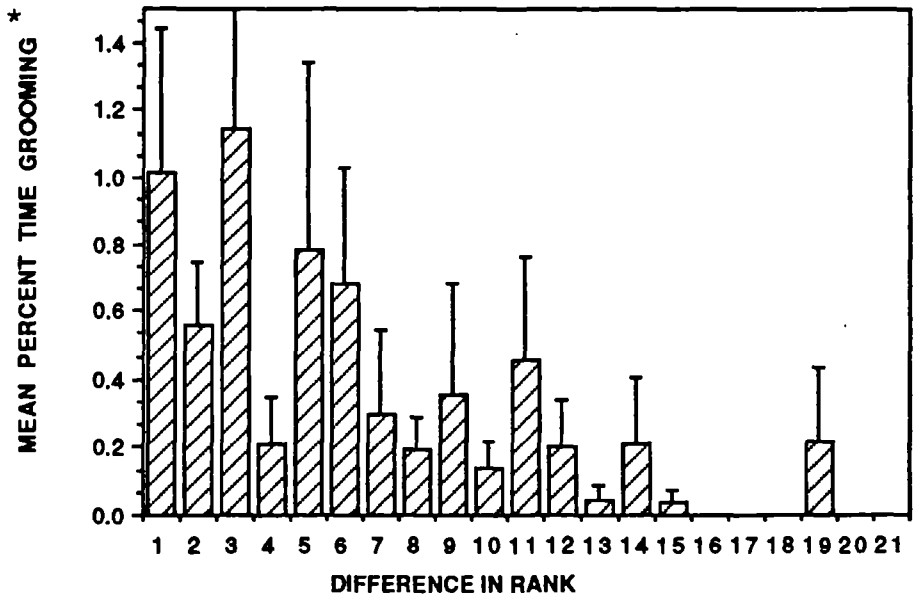
Reproductive profiles of females and rates at which they received affiliative approaches from other females were strongly related. The percentage of months cycling is negatively correlated with the rate at which focal females were approached ($r_s=^{-}0.773$, $p<0.001$), but uncorrelated with the rate at which they approached other females ($r_s=0.078$, $p=0.758$). The correlation between percentage of months cycling and total rate of affiliative approaching is near-significant ($r_s=^{-}0.466$, $p=0.051$). Conversely, females which had black infants received affiliative approaches at a significantly higher rate than those that did not ($t=^{-}4.77$,

df=16, p<0.001), while there was no difference in the rate at which they made affiliative approaches (t=0.04, df=16, p=0.970), nor in the overall rate of affiliative approaching (t=-1.84, df=16, p=0.084).

Females made affiliative approaches to each other far more than they did to males (1.04/hour, compared to 0.02/hour; Chi-square test on raw frequencies, X^2=226.2, df=1, p<0.001). They were also rarely approached in this manner by males (0.06/hour). Thus, the behaviour appears to be particularly associated with interfemale relationships, and rates of male-female approaches were far too low (18 interactions in total) to permit analysis by rank or reproductive state.

(iii) Grooming: Rank was unrelated to the percentage of time focal females spent being groomed by other females (r_s=0.158, p=0.530), the percentage of time grooming them (r_s=0.053, p=0.836), and the percentage of total time involved in grooming with them (r_s=0.102, p=0.686). Neither was rank significantly related to the ratio of grooming received to grooming given in interactions with other adult females (r_s=0.288, p=0.246). This lack of associations between rank and grooming time does not appear to be affected when percentage of months cycling is partialled out (Table 4.1). However, the amount of grooming within dyads was strongly influenced by the difference in rank, more occurring between closely ranked females than between distantly ranked females (r_s=0.848, p<0.001 - see Figure 4.4).

FIGURE 4.4: RELATIONSHIP BETWEEN RANK DIFFERENCE AND PERCENT TIME GROOMING



* Percentage of total activity budget

There is a significant negative relationship between the percentage of months cycling and the overall amount of time being groomed by other females (r_s=⁻0.601, p=0.008). However, females that spent more of the study period cycling do not appear to have significantly reduced the amount of time they spent grooming other females (r_s=0.181, p=0.473), resulting in a near-significant negative correlation between percentage of months cycling and the ratio of grooming received to grooming given in bouts with other females (r_s=0.467, p=0.051).

Females that had black infants during the study received significantly more grooming overall than those that did not (t=⁻5.69, p<0.001), but there was no significant difference in the amount of grooming given by them (t=0.03, df=16, p=0.973). In consequence, females having black infants had superior ratios of grooming received to grooming given in bouts with other females (t=⁻2.80, df=16, p=0.013), and spent significantly more time grooming with them overall (t=⁻2.34, df=16, p=0.032).

Focal females spent slightly more of their time grooming with other adult females than they did with adult males (5.2% versus 3.8%). However, there were fewer potential male than female partners available, and when expected durations are calculated, these match the observed values almost exactly (5.4% and 3.6% respectively). Males received slightly more grooming from females than they gave, (54.3% of all male-female grooming). To examine this trend further, each focal animal was scored according to the relative durations of male-female and female-male grooming; in 19 out of the 26 cases,

the predominant direction of grooming favoured males (x^2=5.538, df=1, p<0.05). There was a near-significant positive correlation between the dominance rank of focal females and the amount of time they spent grooming with adult males (r_s=0.421, p=0.082), and this association does appear to be increased by holding constant the effect of percentage of months cycling (Kendall's tau: r=0.467, partial r_{mc}=0.504). Similarly, percentage of months cycling and time spent grooming with males are positively correlated (r_s=0.545, p=0.019).

(iv) Coalitions and aiding: The data on alliances between females are very sparse, consisting of 15 interactions occurring in focal samples during the main period May-December (about 1 every 13.7 hours of observation) and 18 *ad libitum* observations. Because of this, statistical analysis is not possible, and no firm conclusions can be drawn, but it is nevertheless worth pointing out some suggestive trends in the data. None of these interactions appeared to be directly related to disputes over resources. Of the 33 interactions, the female receiving aid was in the top half of the hierarchy on 14 occasions and in the bottom half on 16; on three occasions it was unclear which individual had aided the other. The female receiving aid ranked higher than the female giving it in 11 and lower in 19 out of the 30 interactions where roles could be assigned. There was a tendency for coalition partners to be close in rank; the mean rank difference of coalition partners was 3.95, and in 20 of the 30 interactions (67%) coalition partners were three or less ranks apart.

However, coalitions between individuals far apart in rank were observed on four occasions, in each case aid being received by the dominant (rank differences of +9,+10,+16 and +21). In summary, the paucity of the data notwithstanding, reasonable evidence exists to suggest that closely ranked individuals (or close kin) were preferred alliance partners, while aid was occasionally given to relatively high-ranking individuals, presumed not to be close kin.

Out of the 30 coalitions, aid was given to cycling females on 15 occasions, to lactating females on 9 occasions, and to pregnant females on 6 occasions. These frequencies do not differ from those expected if aid was given randomly according to the number of "female months" in each reproductive state (X^2=4.566, df=2, p>0.05). The same is true when the reproductive states of donors is considered (X^2=2.44,df=2, p>0.20). Note, however, that, because it was necessary to combine *ad lib* and focal observations to get a reasonable sample size, it was not possible to control for differences in focal sampling time in these calculations.

In focal female samples, coalitions were more frequently made with males than with other females, but rates were still low (n=27, or about one every 7.6 hours, compared with one every 13.7 hours between females). Aid was given to HRFs and LRFs at similar rates (0.06/hour and 0.07/hour).

(c) Discussion of social organisation among females

The findings of these analyses can be summarised as follows:

1) Dominance relations were found to be consistent, and the 26 adult females in the troop could be ranked in a linear hierarchy. The top-ranking female was never observed to lose a dyadic interaction with other females, while the bottom-ranking female was never observed to win one.

2) HRFs acted aggressively or were avoided more frequently than LRFs, and they received aggression or avoided less frequently. There was no apparent relationship between dominance rank and the rate of receiving aggression from and avoiding adult males. Rank was also unrelated to the rates at which focal females affiliatively approached others or were approached by them, and to the amount of time being groomed by other females, the amount of time grooming them, and the ratio of grooming given to grooming received. However, HRFs tended to spend more time than LRFs in grooming with males. Coalition formation between females was infrequent, and no clear pattern of distribution with respect to rank could be discerned. As far as the sparse data can reveal, when coalitions were formed between females not closely related, aid tended to be given "up the hierarchy", to relatively high-ranking females.

3) The difference in rank between adult females (which is assumed to also estimate the degree of relatedness) had a pervasive influence on the distribution of interactions.

Closely-ranking females were involved in more agonistic interactions, spent more time grooming each other, affiliatively approached each other more frequently, and perhaps formed coalitions together more frequently.

4) The reproductive profiles of females during the study period also had important influences on the distribution of interactions. The percentage of months that focal females were cycling was positively correlated with the amount of time they spent grooming with males, but negatively correlated with the amount of grooming received from other females and with the rate at which other females made affiliative approaches to them; however, the amount of time they spent grooming other females, and the rate at which they affiliatively approached them were not significantly affected. Rates of agonistic interactions with both females and males were unrelated to the percentage of months cycling. Females which had black infants during the study period were aggressive to or avoided by other females more frequently than those that did not, but there was no difference in the rate at which they received aggression or avoided; these females also received more grooming from other females, and had superior ratios of grooming received to grooming given.

5) Females groomed each other slightly more than they groomed males, though this difference disappeared once the discrepancy in partner availability was taken into account. Females tended to groom males more than males groomed them.

The above findings are in general agreement with previous studies on baboons and other cercopithecine monkeys. Although authors rarely test statistically for linearity in primate hierarchies, the review by Jackson and Winnegrad (1988) suggests that linearity is the norm, at least amongst cohorts of adult females. The implication of this is that some kind of resource competition is occurring. Agonistic interactions may not always be directly related to resource acquisition, and I specifically excluded feeding supplants from the analyses. The significance of many interactions probably lies in the establishment and maintenance of dominance relations which determine priority of access through their effects on spatial organisation and the tendency of subordinates to avoid conflict with dominants (Rowell, 1966; Robinson,1981; Furuichi, 1983 Collins, 1984). While this kind of view has sometimes been criticised on the basis that "dominance" is actually only an abstraction of patterns of interaction (Rowell, 1974; Hinde, 1978), having no substrate in the minds of the animals themselves, there is now evidence that individuals, on some level, understand their own and others' rank relations (Seyfarth, 1981; Seyfarth and Cheney, 1988; Dasser, 1988). The issues of differential resource acquisition and the mechanisms of competetive exclusion are explored in Chapters 5-7.

One respect in which the findings did not reflect those in other studies was the failure to demonstrate rank-related attractiveness in the distribution of affiliative interactions. A number of authors have found, for example, that, in matrilocal multifemale groups, high-ranking female

engage in a disproportionately large amount of grooming (**Macaques**: Bernstein and Sharpe, 1966; Sade, 1972b; Oki and Maeda, 1973; Rhine, 1972; Silk *et al.*, 1981. **Baboons**; Hall, 1967; Seyfarth, 1976, 1977; Stammbach, 1978. **Vervets**: Seyfarth, 1980; Fairbanks, 1980). Seyfarth (1976, 1980) has developed a model of affiliative relations amongst females, based on the principle of attraction to high rank combined with competitive exclusion, which explains both this finding and the tendency amongst cercopithecines for most grooming to occur between closely-ranking individuals (Seyfarth, *ops cit.*; Kawai, 1958; Sade, 1965, 1967; Koyama, 1967; Bramblett, 1970; Lindburg, 1971; Oki and Maeda, 1973; Collins, 1981; Fairbanks, 1980; Silk *et al.*, 1981; Colvin, 1983b). However, this rank-adjacency effect can also be explained in terms of attraction to kin (either due to kin selection or to the benefits of familiarity, or both - see Colvin, 1983a). Furthermore, a number of studies apart from the current one have failed to demonstrate rank-related attractiveness (Rowell, 1966; Rosenblum *et al.*, 1966; Bernstein, 1970; Lindburg, 1973; Altmann, 1980; Dunbar, 1980; Collins, 1981). Dunbar (*ibid)*, for example, found that most female-female grooming in gelada (*Theropithecus gelada*) occurred between putative kin, and found no evidence for competition to groom HRFs, and Collins (1981), working on wild yellow baboons (*P.cynocephalus*), found that grooming rates among adult females were unrelated to dominance rank. Neither has it been possible to confirm the prediction of Seyfarth's model that the ratio of grooming received to that given will be positively correlated with rank, and that the degree of reciprocity will be greater between closely-ranking individuals (Seyfarth, 1980). Thus,

at best, the principle of attraction to high rank appears not to operate universally amongst female cercopithecines. Seyfarth (1983; Walters and Seyfarth, 1986) points to demographic variation as a possible cause of this lack of consistency, arguing that rank-related attraction will, in fact, be most important in populations where females disperse (such as in *Papio hamadryas*), rather than in matrilocal or female-bonded groups, or else where groups are small, so that individuals tend to have fewer close kin with whom to interact. As Walters and Seyfarth (1986) point out, however, preference for HRFs has not been universally demonstrated even within such groups. One question that needs to be answered is the extent to which the greater amount of grooming received by HRFs (in studies where this has been found) is simply due to the confounding effect of matriline size; if high-ranking matrilines are larger than low-ranking matrilines (as found for macaques by Sade *et al.* 1976; Drickamer, 1974), then HRFs will have more relatives with which to groom than will LRFs. Admittedly this cannot explain Seyfarth's (1976) finding that, within the majority of dyads, the subordinate individual did most of the grooming, nor the finding by Sade (1972b) that the amount of grooming received by individuals was more closely correlated with her rank than with the size of her family.

While Wrangham (1980) cited Seyfarth's principle of rank-related attraction as evidence for feeding competition mediated by dominance, there is no necessary relation between the two phenomena. The argument suggests that subordinates can improve or consolidate their positions by obtaining aid from dominants with whom they form strong affiliative

relationships. Seyfarth and Cheney (1984) have shown that vervet monkeys pay more attention to requests for aid from unrelated individuals who have recently groomed them than from unrelated individuals who have not, so grooming could perhaps be "used" by subordinates to enlist the support of socially powerful allies. However, it seems most likely that individuals will distribute aid optimally in terms of maintaining or improving their own hierarchical position, and that of their relatives, rather than simply in terms of who grooms them; of course the two may coincide to a great extent, because kin selection (Hamilton, 1964) enhances benefits of cooperation when partners are related. In addition, familiarity, which is engendered by kinship, can facilitate cooperative behaviour (Colvin, 1983a). Within dyads of adjacently-ranked females, the value of each as a coalition partner is theoretically unrelated to rank, because each is dominant to the same number of individuals outwith the dyad (i.e. their relative power - Datta, 1983 - is equivalent). Therefore, the prediction concerning the predominant direction of grooming should only apply to individuals more than one rank apart.

The conclusion to be drawn, on both empirical and theoretical grounds, is that high-ranking animals are not necessarily the most attractive as grooming partners. This does not preclude them from being important as allies of subordinates, but this should be the case only in circumstances that benefit HRFs "politically" (sensu de Waal, 1982. See also Noe, 1986, for discussion of game-theoretic approach to modelling the distribution of coalitions in male baboons). In the present

case, the data seem to provide more support for a model of affiliation networks based on attraction to kin, or to familiar individuals (see Colvin, 1983a), than for a competetive exclusion model, although caution is required due to the rather small sample sizes. Relevant to this is the finding by Colvin (1983b) for age cohorts of immature male rhesus monkeys (*Macaca mulatta*); not only was the amount of grooming strongly related to rank similarity or kinship, but amongst adjacently ranked dyads, most grooming occurred within those in which the individuals were particularly closely related.

Like Seyfarth (1976), I found that coalition formation among females was rare (33 observations in 10 months, compared to Seyfarth's total of 32 in 15 months); also like Seyfarth, and a number of other authors (reviewed by Silk, 1986a), I found that coalitions were most often formed between closely-ranking individuals, suggesting kinship as the primary factor once again. Resource competition was never directly implicated in these interactions. It may be that active coalitions occur mainly when dominance relations become unstable, perhaps because of demographic changes. There is evidence from both macaques and baboons that escalated polyadic aggression does indeed increase at such times (Chance *et al.*, 1977; Gouzoules, 1980; Samuels and Hendrickson, 1983; Ehardt and Bernstein., 1986; Samuels *et al.*, 1987). For the rest of the time, coalitions may influence resource competition only rather indirectly, by the implicit threat of aggression against subordinates should they try to supplant dominants.

features relevant to competition. Because of this, I am probably only scratching the surface of the social complexity (for more comprehensive analyses of the dynamics and determinants of social relationships in baboons, macaques and other species, see Hinde, 1983b).

(a) Female dominance hierarchy

The following analysis utilises 532 observations of dyadic agonistic interactions between adult females. These comprise 361 *ad libitum* observations, and 171 observations extracted from focal samples. Excepting supplants over food, all types of agonistic and approach/avoid interactions (see Chapter 2) were pooled and scored according to winner and loser (food supplants are analysed separately in Chapter 7). Using these data it was possible to determine the direction of dominance for 212 of the 325 dyads (65%). Appleby (1983) presents a method for evaluating the linearity of hierarchies, based on the estimated number of circular triads. Using this procedure it is found that a significantly linear hierarchy existed among the STT females ($d=442.75$, $x^2=107.77$, $df=32.2$, $p<0.001$). The coefficient of linearity is only $K=0.392$, lower than any of those presented for four study groups of savannah baboons in the review by Jackson and Winnegrad (1988). However, this cannot be taken as evidence for relatively low linearity in the STT cohort, because the value of K is inversely related to the proportion of undetermined dyads; in the present study this was 34.7%, whereas Jackson and Winnegrad excluded data sets having more than 20% of dyads undetermined.

Interestingly, the distribution of aggressive and approach-retreat interactions among the STT females showed the same pattern as that for affiliative interactions; rates were highest between individuals close in rank, which is perhaps counterintuitive, since these are also likely to have been kin. There are two possible explanations. Firstly, because of the relatively small difference in power (*sensu* Datta, 1983), it is less risky and more worthwhile for subordinates to challenge dominants just above them in the hierarchy, and therefore more crucial for dominants to assert their position. A second, more prosaic, explanation, is simply that the rate of interactions between individuals is directly related to the amount of time they spend in proximity to one another. Relevant to this suggestion is the fact that most of these interactions were of the approach-retreat type (83%), rather than the escalated aggression likely where dominance is at stake.

I found little evidence for systematic persecution of subordinates by gangs of dominants, as in the reproductive competition reported for yellow baboons (*Papio cynocephalus*) by Wasser (1983; Wasser and Starling, 1986), and for gelada (*Theropithecus gelada*) by Dunbar (1980). Overall rates of agonistic interactions were unrelated to the reproductive profiles of females, except that females which had black infants were avoided or were aggressors more frequently than were other females. Only five episodes of apparent "bullying" were observed during the study, in which an individual was repeatedly threatened, chased and bitten by other females. The targets of this aggression were females in the detumescent

phase of the oestrous cycle in two cases, two females whose perineal skin was in the early stages of swelling, and one pregnant female. The episodes lasted between about five minutes and thirty minutes, and in one case the aggression recurred at intervals throughout the day. It is possible that these incidents were associated with reproductive competition, but the rates were so low that a significant impact on reproductive profiles of females in the group generally is doubtful. In no case was it possible to link disruption of sexual cycling or pregnancy to these attacks.

Because male baboons are so much larger than females, they may have particular importance both as allies and as potential aggressors, compared to the situation in other species (Smuts, 1985, Dunbar, 1988). Amongst non-human primates, "special relationships" (Ransom and Ransom, 1971) between adult females and males, that persist throughout the reproductive cycle, have been found in baboons, macaques and woolly spider monkeys (*Brachyteles arachnoides*), but not in vervets (Smuts, 1985). The benefits of such relationships for females (see Smuts, 1983) may result in the somewhat unusual situation of females competing amongst themselves for access to males (see Dunbar and Sharman, 1983). Seyfarth (1976) found that in 31% of approach-retreat interactions, and in 93% of actively aggressive interactions between adult females, competition over males was implicated (data from Seyfarth's Table IV). In her study of *Papio anubis* at Gilgil, Kenya, Smuts (1985) found that HRFs had more male friends than did LRFs, and that rank was related to the age and residency status of male friends. She also found that females groomed males more

frequently than they were groomed by them, regardless of reproductive state (76-87% of bouts), a result which has also been obtained in a number of studies of Old World monkeys (**Baboons**: Hall, 1962; Saayman, 1971a; Hausfater, 1975. **Macaques**: Kaufman, 1965; Lindburg, 1967; Oki and Maeda, 1973; Sugiyama, 1971; Angst, 1975. **Mangabeys**: Chalmers, 1968. **Guenons**; Rowell, 1974). In the present study it was found that female rank correlated positively, though weakly, with the amount of time spent grooming with males. The bias towards females grooming males more than the reverse was also apparent, though the effect was not so strong as in Smuts' study. There was a positive association between the percentage of months cycling and the amount of time spent grooming with males; this can be explained by the fact that much grooming occurs between males and females when the latter are sexually receptive, during consortships. Conversely, the negative association between percentage of months cycling and the amount of time being groomed by other females suggests that time taken up by relationships with males during consortships compromises time investment in other relationships. Nevertheless, the amount of time focals spent grooming other females was unrelated to the percentage of months cycling, whereas the total amount of time spent grooming all partners was positively correlated with this variable, a pattern parallelled by the variation in rates of affiliative approaches; this raises the possibility that cycling females increase the level of their investment in affiliation generally, in order to maintain important relationships that would otherwise suffer from lack of "servicing" during periods of sexual activity.

Byrne *et al.* (in press) compared female-female and female-male bonding in mountain chacma baboons (*Papio ursinus*), finding that the latter was stronger than the former; rates of affiliative interactions across matriline boundaries were low and the distribution of grooming was significantly male-biased compared to the expected (random) distribution. Byrne *et al.* argued for a clear distinction between matrilocality (females remain in natal troop) and female-bonding (groups are founded on female-female affiliative networks). They suggested that all baboons are better classified as "cross-sex-bonded" than female-bonded, in contrast to other Old World monkeys, such as vervets (*Cercopithecus aethiops*), which do not show strong male-female affiliative relationships. In the present study, females groomed each other more than they groomed males, but the distribution was not biased when the difference in availability of partners of each sex was taken into account. Affiliation between females was strongly related to closeness in rank, or relatedness, and no evidence could be found for specific attraction to high-ranking individuals. Thus it could be argued that the group was cross-sex-bonded rather than female-bonded. However, the taxonomy proposed by Byrne *et al.* does not necessarily constitute a hard-and-fast dichotomy; there is no reason why groups should not be both female-bonded *and* female-male bonded. Indeed, it is possible that the two types of bonding are closely related, in that, as mentioned, the large size of male baboons may make them particularly valuable as allies for females in competition with one another. The results presented in this chapter indicate the occurrence of such competition, and subsequent

chapters demonstrate its ecological importance. Further work may eventually reveal a role for males in the regulation of this competition, thus perhaps explaining the lack of female-male bonding in some undimorphic species.

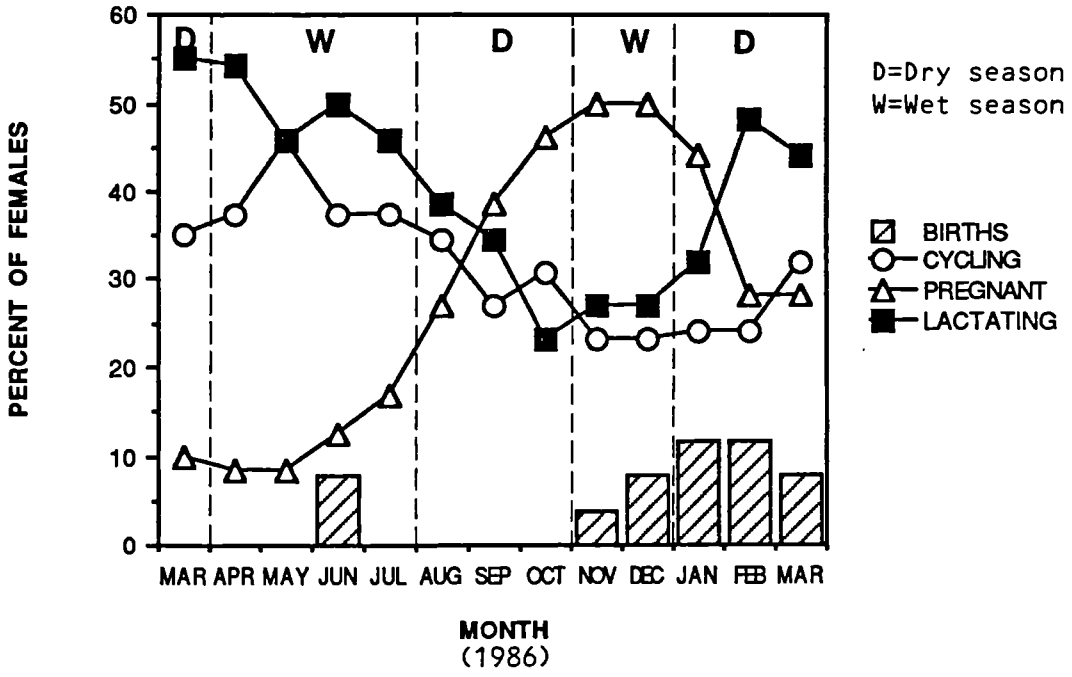
3) REPRODUCTION AND BODY CONDITION

In this section I present data on variation in the number of females in different reproductive states during the course of the study, and on monthly and reproductive-state specific variation in body condition. The study was too short to permit any extensive examination of variables like the duration of post-partum amenorrhea and interbirth intervals, or the influences of resource availability and dominance rank on these - such analysis must await long-term data. However, the data that are available will be discussed in relation to findings from long-term studies on other populations.

(a) The timing of reproduction

Changes in the number of females in each reproductive state (cycling, pregnant and post-partum amenorrhea), and the number of births in each month between March 1986 and November 1987 are shown in Figure 4.5. (additional data from D.Lochhead). It can be seen from this that there was no strict seasonality in the timing of reproduction. However, there does seem to have been something of a birth peak between December 1986 and

FIGURE 4.5: REPRODUCTIVE PROFILE OF STUDY TROOP (1986/87)



March 1987. The two females that gave birth prior to that period, in June 1986, were both young, primiparous animals.

The duration of post-partum amenorrhea is known for six individuals; the mean was 11.0 months (standard deviation=1.41). This figure is slightly less than those reported from other populations (Altmann *et al.*, 1988; Amboseli = 12months. Nicolson, 1982; Gilgil = 14 months). The month of infant pelage transition from black to more than 50% mottled brown was also recorded for 6 individuals; in four cases this occurred in month five after parturition, and in two cases during month six (mean=5.33 months, standard deviation=0.52). This accords with observations on infants at Amboseli, for which the transition occurs between months 3-6 (Altmann, 1980). For this parameter the Gilgil data again suggest relatively retarded development, with the transition reported to occur around month seven. These parameters however are not fixed within populations, but probably depend to a great extent on food availability at particular times (e.g Strum and Western, 1982).

(b) Female and infant mortality

It is not valid to calculate mortality rates for such a short study duration. The main study period was probably a time of comparatively low environmental stress for the baboons (judging by drought periods immediately before and since), and only two females died or disappeared during the ten months between March-December 1986. One of these disappeared at the end of the first dry season, when a number of animals, including this one, did appear to be in poor condition. The

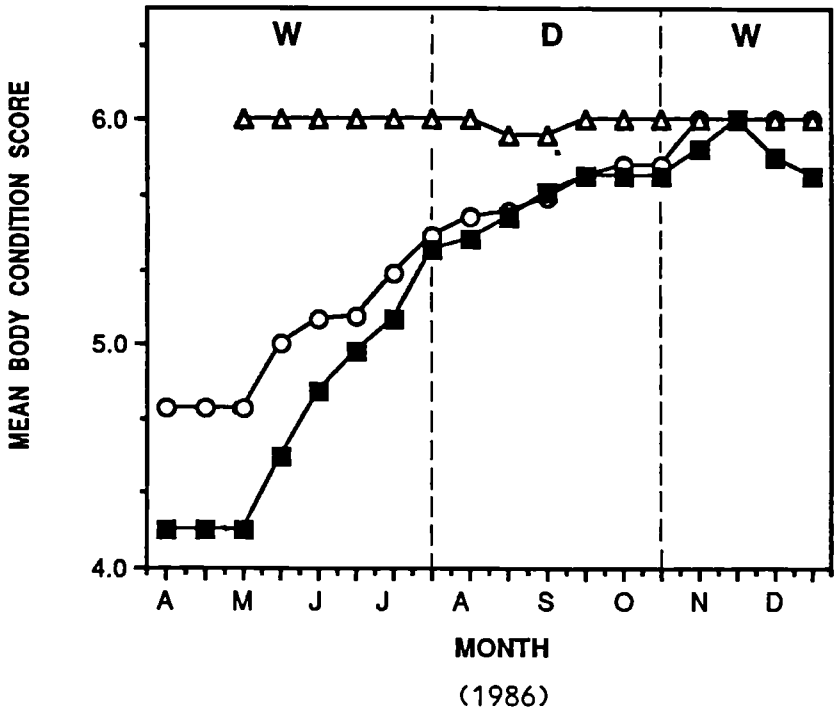
other female died about 24 hours after receiving severe injuries, in the form of bruising, lacerations, and suspected fractures, perhaps as a result of an encounter with a predator. Similarly, only two infants died or disappeared between March 1986 and March 1987: one of these was an infant of 5-6 months (transitional pelage), in May 1986; the other, born in February 1987, was only two days old, being one of three successive neonatal casualties of the female KH (she was observed carrying a dead neonate at the beginning of the study, in January, 1986, and again in March 1988 - presumably some congenital problem is implicated here).

(c) Female body condition

Figure 4.6 shows changes in the mean body condition of females in each reproductive state for the period April-December 1986 (no data are available for the early part of 1987). Pregnant females were, according to the index, at or near peak condition throughout, whilst cycling and lactating females show a sustained gradual improvement from the post-drought low at the beginning of the sampled period, through to December. Lactating females (or, at least, those in post-partum amenorrhea) were initially worse off than cycling females, but had caught up by September.

Figure 4.7 plots mean body conditions of females for each month of the reproductive cycle, between eight months before parturition (about two months before conception) and 12 months after that time. Data for females in the top and bottom halves of the hierarchy are plotted separately. There is an indication that females only became pregnant after reaching a

FIGURE 4.6: BODY CONDITION CHANGES OF FEMALES

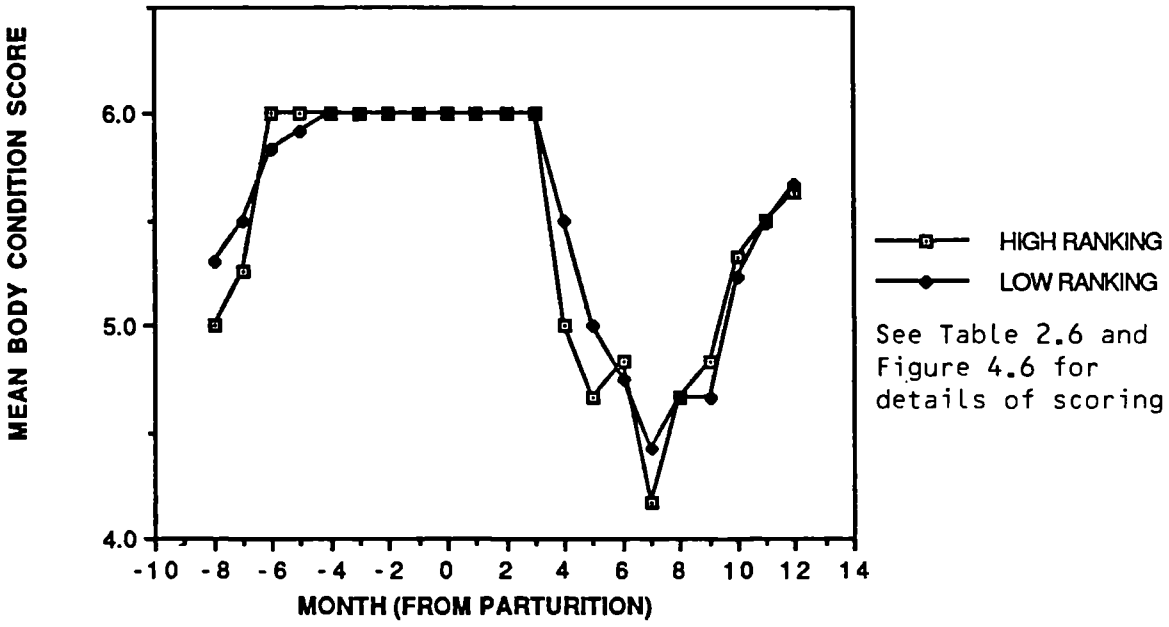


W=Wet season
D=Dry season

CYCLING
PREGNANT
LACTATING

Body condition assessed according to thinness and hair loss, on a scale from 2-6 (see Table 2.6).

FIGURE 4.7: BODY CONDITION CHANGES OVER REPRODUCTIVE CYCLE FOR HIGH AND LOW RANKING FEMALES



certain level of body condition. Subsequently, throughout pregnancy, a high level was maintained. Starting at three to four months after parturition, there was a visible decline in condition, continuing until month seven. After this, condition rises towards pre-conception levels. No consistent effect of dominance rank is apparent.

Discussion of reproduction and body condition

Baboons, along with some macaques, chimpanzees and gorillas are not obligate seasonal breeders (Lancaster and Lee, 1965; Altmann, 1983). This is probably because they exceed the maximum body size permitting interbirth intervals of one year or less (body size and interbirth interval are positively correlated across species - Harvey and Clutton-Brock, 1985). The body size difference between baboons and vervets, which often occupy very similar habitats and have overlapping home ranges, may explain why the latter are seasonal breeders (Whitten, 1983; Cheney *et al.*, 1988), while the former are not. In fact, since interbirth intervals are often close to two years in baboons (19-28 months at Gilgil; Strum and Western, 1982. 21 months at Amboseli; Altmann, 1983) it is a moot point as to why there is not a biennial cycle, with some individuals giving birth one year, and others the next. It is possible that lack of predictability in the phenology of baboon plant foods is the answer; as we have seen in Chapter 3, the availability of food is closely linked to rainfall, and annual rainfall is known to vary considerably from year to

year in savannah ecosystems (Delaney and Happold, 1979). For this argument to hold water, however, it would be necessary to show that the foods eaten by seasonally-breeding vervets are more predictable than those eaten by baboons. Perhaps the most likely explanation, therefore, is simply that any benefits of synchronising the major energetic costs of reproduction with seasonal food peaks are offset by the cost that would be engendered by delaying the next pregnancy. This delay would amount to 7 months in the present case, assuming that it takes 17 months from conception to weaning (6 months pregnant plus 11 months of lactational amenorrhea).

Altmann (1983) noted that the seasonal pattern of food availability nevertheless resulted in a tendency towards birth seasonality in yellow baboons (*Papio cynocephalus*) at Amboseli National Park, Kenya. Females tended to conceive more readily in the rainy season, when food was assumed to be relatively abundant; this meant that they tended to give birth at a time of low availability, but that the stage of probable maximium energetic stress (around six months after parturition) coincided with the following rainy season, when food availability was again presumed to be high. In the present study, the majority of conceptions occurred at the end of the long rainy season and beginning of the ensuing dry season, resulting in a birth peak during the dry season between January and March. The trough in body condition which STT females experienced around months six to seven supports Altmann's suggestion that this is a critical point for mothers and infants. This point would be reached in June or July, during the long rains, for females giving birth in January and

February. There is therefore also limited support for Altmann's suggestion that seasonal birth peaks are linked to food availability at critical periods of the reproductive cycle. Lee (1987) has also shown that the period of peak lactation in vervet monkeys (*Cercopithecus aethiops*) coincides with the period of peak food availability. However, the birth peak in the present case was quite extended, with an equal number occurring in May as in January, for example (Lochhead, pers. comm.); these mothers would have experienced maximum stress around October/November, when overall food availability could be expected to be at its lowest (although diet quality at this time was high - see Figure 6.4). It is therefore perhaps more likely that these slight birth peaks result directly from a tendency of females to conceive subsequent only to exceeding some threshold of body condition. Functionally, it makes no sense for a female to resume sexual cycling and to become pregnant again if she does not have sufficient reserves to bear the physiological stress involved. Studies on a number of species, including humans, have shown a relationship between nutritional status and the probability of ovulation or conception (Sadleir, 1969; Belonje and van Niekerk, 1975; Frisch, 1982), and STT females became pregnant only in the upper range of body condition values.

The data on changes in body condition during the course of the reproductive cycle confirm Altmann's (1981, 1983) suspicion that females are unable to compensate entirely for the energetic costs of lactation by increasing the amount of time spent feeding. Similarly, Hazama (1964) found that female Japanese macaques (*Macaca fuscata*) steadily lost weight during

lactation. The data presented here also suggest, however, that the extent to which females are affected is dependent on environmental factors, since seasonal changes in food availability also influenced body condition. The two females which gave birth in the middle of the study, and whose period of maximum stress therefore coincided with high food availability, exhibited barely any decline in condition. In contrast, mortality during the drought of 1988 was concentrated among females with young infants (Saunders, pers. comm.), an observation supported by more long-term patterns at Amboseli (Altmann *et al.*, 1988). Experimental work, on baboons in captivity, also suggests a relationship between resource availability and the ability of females to maintain condition during lactation; mothers given 80% of their *ad libitum* intake maintained their milk output at normal levels and lost little weight, while those on 60% of the *ad libitum* diet showed reduced milk output and substantial decline in weight (Roberts *et al.*, 1985). Growth rates of captive baboon infants studied by Buss and Reed (1979) were related to experimentally manipulated protein levels in maternal diets. In white-tailed deer (*Odocoilus virginianus*) mortality of fawns varied according to the amount of protein in the diet of mothers; those on low-protein diets usually experienced complete lactational failure (Murphy and Coates, 1966). Further work is required, involving more precise measurements of nutritional status, to evaluate the influence of environmental variation on the tendency of nursing mothers to lose condition.

Mori (1979) found that the offspring of high-ranking female Japanese macaques were heavier and had higher survival rates than those of LRFs. The amount of body fat on female rhesus monkeys (*Macaca mulatta*) was found by Small (1981) to be related to dominance rank, and a similar result was obtained for body weights of female vervet monkeys (*Cercopithecus aethiops*) by Whitten (1983). In the present study, High- and low-ranking females did not differ significantly in their mean values for body condition through the reproductive cycle. However, the sample sizes were small, and it was not possible to control for confounding effects of age and parity. Long-term data should answer the question of whether or not HRFs in this population are generally able to maintain better condition, and thereby reduce interbirth intervals and/or extend their reproductive lifetimes. However, strong indications on this issue could be obtained from an analysis of individual differences in diet and nutrient intake rates; is there any relationship between dominance and nutrition, and if so, what? These questions are amongst those examined in the following chapters.

CHAPTER 5: DIET SELECTION

1. INTRODUCTION

Primates are selective feeders; they eat a relatively small proportion of the plants that are available to them (Clutton-Brock, 1977). The principle reason for this is that potential food items vary in their chemical composition and digestibility. Protein, simple sugars and storage carbohydrates have been associated with positive selection, whilst fibre and secondary compounds such as condensed tannins and perhaps some alkaloids seem to be avoided (Hladik, 1978; Wrangham and Waterman, 1981; Waterman, 1984). However, there may be considerable species differences in what can be incorporated into the diet; gorillas, for example, are probably unique in consuming large quantities of rotten wood (Goodall,1977). Furthermore, within the range of food items taken by a given species, there may be great variation in the suitability (quality) of items, stemming from differences in the relative proportions of constituent compounds. However, the profitability of particular items will be a function not only of their nutritional quality, but also of the associated time and energy costs of obtaining them (Krebs, 1978). High-quality items should always be taken when encountered (Krebs *et al.*, 1977), but they may not be encountered very often. Abundance may influence representation in the diet both through random encounter rates, and through active "decision rules" (Krebs, 1978) based on the profitability of foraging for specific foods. Thus, relative abundance should play an

important role in determining the composition of primate diets (Gaulin, 1979).

What primates eat, and why, has been the subject of considerable interest. In part this is due to the hope that comparative studies will help us to understand the ecology and behaviour of early hominids, and perhaps even of *Homo sapiens sapiens* (e.g. Jolly, 1970; Dunbar, 1984b; Gaulin and Konner, 1977; Harding and Teleki, 1981; Kinzey, 1987; Sussman, 1987). More generally, diet and dietary selectivity are seen as underlying species differences in other aspects of behaviour and demography, such as territoriality, ranging patterns, and the size, structure and internal organisation of social groups (Crook and Gartlan, 1966; Eisenberg *et al.*, 1972; Clutton-Brock and Harvey, 1977; Wrangham, 1979, 1980). Thus the study of diet is integral to understanding the adaptive principles governing socioecological systems. In the context of the present study, its particular importance derives from two major sources.

(i) Characterising baboon diets: While a considerable amount of research has been conducted on the determinants of diet in certain species, notably the colobine monkeys (e.g. McKey *et al.*, 1981 ; Davies *et al.*, 1988; Waterman *et al.*, 1988), relatively little is known about this in baboons, or indeed in monogastric primates generally. The high proportion of plant reproductive parts in the diets of many cercopithecines (Clutton-Brock and Harvey, 1977) has led to the widespread assumption that, as a taxon, they can be characterised with reasonable accuracy by the label "frugivore". The *Papio* baboons are recognised as being

ecologically quite different, the great breadth of their diet being reflected in their usual categorisation as "omnivores" (Altmann and Altmann, 1970; Gaulin and Konner, 1977; Hamilton *et al.*, 1978; Post, 1982; Norton *et al.*, 1987). It is also true, however, that emphasis is sometimes placed on a supposed tendency to frugivory. For example, Richard (1985) states that "olive baboons are frugivorous" in parts of their range, whilst Dunbar (1988) describes the genus as being omnivorous "with a marked preference for fruit", and contrasts the diet of gelada (*Theropithecus gelada*) with the "more frugivorous diet of *Papio* baboons" (Dunbar, 1977). These statements are, of course, quite correct given the dietary classifications currently used by primatologists. If such classifications are to make sense, however, we need to be sure that the categories have reasonable botanical and phytochemical homogeneity. In the case of "fruit", the usual implication is that we are talking about the fleshy, fructose-containing varieties (mainly berries and drupes) which "want" to be eaten in order to have their seeds dispersed, and which are a rich source of energy (Richard, 1985). In comparative studies (e.g. Clutton-Brock and Harvey, 1977; Sailer *et al.*, 1985), however, these are rarely, if ever, differentiated from the drier, less digestible achenes and capsules, or , for that matter, from leguminous pods and seeds, all of which enter into the diets of baboons (Harding, 1973; Hamilton *et al.*, 1978; Post, 1982; Norton *et al.*, 1987). A further point to make here is that the characterisation of the *Papio* baboons as generalists has tended to obscure the fact that they are also highly *selective* (Post, 1981, Norton *et al.*, 1987; Whiten *et al.*, 1987).

(ii) Investigation of individual differences: Analysis of the chemical composition of dietary items, and the factors affecting selection, facilitate the evaluation of nutritional differences between males and females, and the identification of constraints operating on females at different stages of the reproductive cycle. These analyses also provide a framework for interpreting the effects of competition between individuals, investigated in Chapter 6.

In what follows I begin by presenting data on the chemical composition of items, and evaluate common assumptions concerning differences in the "quality" of particular classes of food. Unfortunately it has not been possible to analyse levels of simple sugars, but a gross botanical classification of fruits, separating, among other things, sugary from non-sugary types, is possible. I also examine the relationship between abundance and nutritional composition of different foods, since any such relationship is expected to influence the relative profitability of items for males and females (Demment, 1983). I then describe the overall composition and diversity of the diet and seasonal variation in these factors. The relationships between diet diversity and dominance rank, gender and reproductive effort are analysed. Finally, I examine the phytochemical determinants of dietary selectivity.

2. PHYTOCHEMISTRY

The raw phytochemistry data are presented in Appendix 2. These data are summarised in Tables 5.1 (water, protein, fibre

and lipids) and 5.2 (secondary compounds), in which average percentages are given for the major food classes. Table 5.3 contains details of the species and parts containing alkaloids. The main uses of these data are in building nutritional profiles for individuals by gender, reproductive state and rank, for the assessment of seasonal trends in nutrition, and for analysing the determinants of diet selection. These topics will be pursued in the following sections and chapters. It is, however, worth making two points before moving on; these concern the nutritional quality of particular food types, and the relationship between quality and abundance.

(a) Nutritional quality

Assumptions about the nutritional quality of different food types abound in the primatological literature. In comparative studies foliage is usually considered to be the least nutritious component of diets, notwithstanding the occasional bit of bark or soil, and the proportion of foliage in the diet has been found to be positively correlated with body size (Clutton-Brock and Harvey, 1977; Sailer *et al.*, 1985). Fruits and other reproductive parts are often assigned an intermediate position between leaves and animal matter (Sailer *et al.*, 1985; Hamilton *et al.*, 1978), and the folivore/frugivore dichotomy has been widely used in ecological classifications of primate species (Clutton-Brock and Harvey, 1977a,b,1981; Martin, 1981). It has been argued, for example, that folivores are likely to have relatively low basal metabolic rates, because energy capture

TABLE 5.1: WATER[1] AND NUTRIENT[2] CONTENT OF MAJOR FOOD CLASSES

	Water	Protein	Fibre	Lipid	N[3]
A. Photosynthetic parts					
Grass blades	78.7 (4.3)	24.4 (8.2)	24.9 (4.2)	7.6 (1.9)	4
Grass stolon meristem	80.0 (-)	30.4 (-)	17.6 (-)	9.0 (-)	1
Herb leaves	84.2 (8.3)	27.6 (6.3)	16.6 (6.6)	n.a. (-)	6
Shrub leaves	86.2 (6.7)	28.2 (9.6)	11.4 (3.8)	n.a. (-)	3
Acacia leaves	75.0 (-)	42.8 (-)	10.2 (-)	8.0 (-)	1
Tree leaves	77.8 (-)	27.1 (-)	10.4 (-)	n.a. (-)	1
B. Storage parts					
Sedge bulb	82.1 (5.5)	9.1 (0.7)	16.6 (2.6)	5.0 (2.8)	2
Sedge corm	39.0 (-)	5.8 (-)	1.3 (-)	3.0 (-)	1
Herb root	71.4 (0.8)	5.8 (0.9)	26.8 (4.2)	6.0 (-)	2
Herb bulb	84.9 (-)	18.3 (-)	12.7 (-)	6.0 (-)	1
Sansevieria leaf base	93.2 (-)	15.8 (-)	16.9 (-)	8.0 (-)	1
C. Flowers					
Grass flower	71.3 (7.6)	12.6 (2.3)	29.0 (7.5)	n.a. (-)	3
Herb flower	87.8 (3.4)	19.5 (6.2)	17.4 (1.9)	10.5 (-)	5
Acacia flower	71.7 (5.8)	22.2 (5.7)	11.9 (3.6)	8.1 (1.2)	3

TABLE 5.1, cont.

	Water	Protein	Fibre	Lipid	N[3]
D. Fruits/seeds					
Berries	80.6 (8.9)	12.3 (0.9)	27.4 (14.7)	3.5 (3.5)	4
Dry fruits (achenes, capsules etc.)	69.2 (7.9)	15.5 (5.1)	28.8 (10.8)	5.6 (4.5)	9
Acacia					
a. Dehiscent pods					
fresh pods+seeds	68.7 (9.1)	23.5 (5.8)	26.4 (4.2)	3.9 (0.6)	3
dry seeds	12.5 (-)	37.4 (-)	16.9 (-)	12.5 (-)	1
b. Indehiscent pods					
fresh pods-seeds*	64.6 (5.1)	12.3 (1.9)	26.3 (13.5)	4.0 (1.4)	3
fresh seeds	66.4 (4.1)	28.7 (1.1)	15.3 (3.4)	3.5 (0.7)	2
fresh seed kernels	74.5 (0.1)	47.7 (0.9)	3.7 (1.1)	9.5 (2.8)	2
fresh seed skins*	66.9 (0.2)	13.5 (2.2)	22.2 (0.7)	3.5 (0.7)	2
E. Other					
Euphorbia stems	89.9 (1.2)	9.9 (3.3)	21.2 (7.0)	9.0 (1.4)	2
Mushrooms	66.7 (-)	9.2 (-)	n.a. (-)	n.a. (-)	1
Acacia green thorns	78.1 (-)	26.2 (-)	15.1 (-)	n.a. (-)	1
Aloe flower stem	90.6 (-)	8.4 (-)	24.7 (-)	n.a. (-)	1

Notes:
Figures are means for food classes, figures in brackets are standard deviations.
[1] Percentage of total weight
[2] Percentage of dry weight
[3] Number of species sampled
* Part usually rejected

TABLE 5.2: SECONDARY COMPOUND CONTENT[1] OF MAJOR FOOD CLASSES

	Tannins[2]	Phenolics[3]	Alkaloids[4]	N[5]
A. Photosynthetic parts				
Grass blades	0.5 (0.9)	1.4 (0.1)	0	4
Grass stolon meristem	0.0 (-)	1.2 (-)	0	1
Herb leaves	1.8 (1.7)	2.4 (1.3)	+	6
Shrub leaves	0.0 (0.0)	1.9 (2.3)	0	3
Acacia young leaves	5.3 (-)	10.5 (-)	+	1
Tree young leaves	1.4 (-)	0.9 (-)	0	1
B. Storage parts				
Sedge bulb	6.4 (1.3)	1.0 (0.1)	0	2
Sedge corm	0.9 (-)	0.4 (-)	0	1
Herb root	3.2 (2.0)	7.8 (0.9)	0	2
Herb bulb	0.0 (-)	2.9 (-)	+	1
Sansevieria leaf base	0.0 (-)	0.7 (-)	n.a.	1
C. Flowers				
Grass flower	0.8 (1.1)	1.4 (0.9)	0	3
Herb flower	1.6 (2.3)	3.6 (2.8)	0	6
Acacia flower	3.0 (1.2)	4.8 (1.5)	+	3

TABLE 5.2, cont.

	Tannins[2]	Phenolics[3]	Alkaloids[4]	N[5]
D. Fruits/seeds				
Berries	0.3 (0.6)	2.0 (0.9)	+	4
Dry fruits (achenes, capsules etc.)	0.3 (0.6)	1.1 (0.6)	0	9
Acacia				
a. Dehiscent pods				
fresh pods+seeds	8.9 (7.5)	4.8 (3.2)	+	3
dry seeds (ground)	1.0 (-)	0.7 (-)	n.a.	1
b. Indehiscent pods				
fresh pods-seeds*	6.1 (3.3)	6.4 (0.8)	+	3
fresh seeds	6.9 (3.7)	2.7 (1.2)	0	2
fresh seed kernels	0.6 (0.2)	0.5 (0.1)	0	2
fresh seed skins*	15.0 (4.2)	8.0 (0.2)	0	2
E. Other				
Euphorbia stems	0.0 (0.0)	1.5 (1.0)	0	2
Mushrooms	0.0 (-)	0.0 (-)	n.a.	1
Acacia green thorns	0.0 (-)	5.6 (-)	n.a.	1
Aloe flower stem	0.0 (-)	0.8 (-)	0	1

Notes:

Figures are means for food classes, figures in brackets are standard deviations

[1] Percentage of dry weight
[2] Condensed tannin
[3] Total phenolics
[4] Presence or absence: +=present in at least one sample; 0=not present in any samples
[5] Number of species sampled
* Part usually rejected
n.a. Information not available

TABLE 5.3: PLANT FOODS CONTAINING ALKALOIDS

Acacia brevispica	
Immature leaf	+++
Fresh pod (dehiscent) with seeds	+
Acacia nilotica	
Fresh pod (indehiscent) no seeds	++
Flowers*	+
Acacia mellifera	
Fresh pod (dehiscent) with seeds	+
Flowers	++
Ammocharis tinneana	
Leaf	+++
Solanum incanum	
Green fruit	+
Ripe fruit	++
Herb spp.	
Bulb	+

+++ = high levels, ++ = medium levels, + = low levels
* Not eaten

from leaves is expected to be less efficient than that from fruits (Martin, 1981; McNab, 1980; Muller *et al.*, 1983). With regard to other plant parts, Sailer *et al.* (1985) assume storage and structural parts to be inferior in their analysis of the relationship between body size and diet quality. On an intraspecific level, Demment (1983), argues that foliage represents a relatively high-fibre food for baboons, and is therefore eaten less by females than by the larger-bodied males.

What evidence, then, is there that the foliage eaten by STT represented a high-fibre, low-quality resource compared to fruits and other reproductive parts? The fibre (ADF) measurements for the various types of foliage range from a mean of 10.24%, for *Acacia* leaves, to a mean of 24.9% for grass blades. The mean values for berries and for dry fruits are both above this range of variation (27.4% and 28.8% respectively). The maximum ADF value for any foliage item eaten by the baboons is 28.5% (for the leaves of the vine *Neonotonia wightii*) whereas for fruits it is 48.45%, for the achenes of *Osteospermum vaillantii*. Moreover, five out of the ten commonly eaten species of fruit have ADF values over 30%. Reference to Table 3.1 reveals that foliage was relatively high in protein; in terms of both protein and fibre levels, individual *Acacia* seeds are clearly the highest quality food (assuming protein to be "good" and fibre to be "bad" - see section 5.4 below). The whole dehiscent pods of the species in which these were eaten, however, are, if anything, inferior to the foliage samples.

These results do not support the belief that foliage eaten by baboons is generally a high-fibre (and therefore low-quality) food in comparison with fruits. Demment's (1983) calculations of the proportion of the diets of adult male and female baboons that was made up of high-fibre items was based on the assumption that grass blades and the leaves of herbs, shrubs and trees were high in fibre, whilst flowers, fruits, *Acacia* seeds, exudate, grass seedheads, grass and sedge corms, roots and animal matter were assumed to be low in fibre. It appears that these assumptions are extremely questionable, especially considering that there is substantial overlap between major plant species utilised by baboons in Post's study and by those in my own study (6 genera and 7 species). Of the items supposed by Demment to be low in fibre, only *Acacia* seeds, exudate and perhaps corms are clearly likely to have been lower in fibre than foliage. Corms are also a problematic category in this respect; the way the term is used by researchers at Amboseli (Altmann, pers. comm.) appears to include bulbs (swollen leaf bases) as well as true corms (swollen stems), and these two have rather different phytochemical profiles (Table 5.1). Corms are extremely low in fibre, but bulbs are equivalent to herb leaves in my sample (therefore intermediate between grass blades and foliage of larger plants). Neither corms nor bulbs contain as much protein as the foliage samples, although, being storage organs, they are presumably rich in starch (Waterman, 1984).

Phytochemistry data have recently become available for plant foods at Amboseli (Altmann *et al.*, 1987). Conversion of their

protein results from percentage of wet weight to percentage of dry weight reveals fairly good agreement between their results and those obtained here for the same species and parts. For example, the mean protein content of 20.7% for *Acacia tortilis* flowers calculated from Table 1 in Altmann *et al.* corresponds to a value of 19.1% obtained here (Appendix X). Their value of 29.5% protein for the stolon node meristem of *Cynodon dactylon* is very close to my value of 30.4% for the item. Not all our results are in such close agreement, but the discrepancies are generally reasonably small. In the case of fibre, the measure obtained by Altmann *et al.* was crude fibre, which is not directly comparable to ADF. Nevertheless, evaluation of differences within their sample generally supports the conclusions arrived at above; leaf foods are generally higher in protein, and often lower in fibre, than fruits and some corms.

Perhaps a better indication of the overall quality of food items can be obtained by combining phytochemical measures into single indices. McKey *et al.* (1981) showed that the ratio protein/(fibre+condensed tannins) correlated better with selection in *Colobus satanas* than did any of the constituents on their own. Previewing the results in section 5.3 below, a similar situation obtains in the present case. There is therefore at least some validity in assessing the relative quality of items according to this ratio. In Table 5.4 I present ratios for each of the major food types under the categories of reproductive, photosynthetic, storage and structural parts. The average ratios for each category

TABLE 5.4: FOOD QUALITY RATIOS (PROTEIN/(FIBRE+CONDENSED TANNINS)) FOR DIFFERENT PLANT PARTS.

REPRODUCTIVE	PHOTOSYNTHETIC	STORAGE	STRUCTURAL
1)11.09	9) 2.76	15) 2.64	20) 1.74
2) 2.09	10) 2.47	16) 1.44	21) 0.47
3) 1.49	11) 2.30	17) 0.93	22) 0.34
4) 1.03	12) 1.73	18) 0.40	
5) 0.67	13) 1.50	19) 0.19	
6) 0.53	14) 0.96		
7) 0.42			
8) 0.42			
MEAN 2.22	1.95	1.12	0.88
S.D 3.63	0.67	0.98	0.77

1=*Acacia* seed kernels, 2=*Acacia* dry seeds, 3=*Acacia* flowers, 4=Herb flowers, 5=*Acacia* indehiscent pods+seeds, 6=dry fruits, 7=grass flowers, 8=berries, 9=*Acacia* young leaves, 10=shrub leaves, 11=tree leaves, 12=grass stolon meristems, 13=herb leaves, 14=grass blades, 15=sedge corms, 16=herb bulbs, 17=*Sansevieria* bases, 18=sedge bulb, 19=herb root, 20=*Acacia* green thorns, 21=*Euphorbia* fleshy stems, 22=*Aloe* flower stems.

suggest the following descending rank-order; reproductive parts, photosynthetic parts, storage parts, structural parts. If Acacia seed kernels, which are an extreme outlier, are removed from the calculation, this relegates reproductive parts to a position intermediate between storage and structural parts. Variation between groups in the ratios (with storage parts removed due to small sample size) is not significant (Kruskal-Wallis test; $X^2=3.938$, $p=0.140$. Non-parametric test used because variances could not be stabilised by data transformation).

It is clear that there are grounds for questioning common assumptions about the relative quality of different food items, at least within the dietary range of savannah baboons. This does not mean, of course, that we should simply turn the

usual dichotomy around, and consider fruits to be a low-quality category. For one thing, as noted, it all depends on what type of fruit is concerned; the fruits eaten by arboreal guenons and ceboids, for example, mostly *are* the fleshy sugar-rich variety (Coelho *et al.*, 1976; Gaulin and Konner, 1977; Gautier, 1988), whereas the leaves eaten by colobines are undoubtedly higher in fibre and lower in protein than those analysed here (c.f. data in Mckey *et al.*, 1981; Waterman *et al.*, 1988; Davies *et al.*, 1988). Perhaps really definitive statements about species differences in diet quality and nutrient intake must await the production of phytochemical profiles across a range of species. With respect to intraspecific trends, another complication is with the notion of a unitary dimension of quality; while the assumption that protein=good and fibre=bad probably has general validity, this should not obscure the fact that animals require a variety of nutrients, including also lipids, carbohydrates, vitamins and minerals, and these may be obtained from a wide array of food types. Relatively recently, the importance of dietary fibre for health in humans has been highlighted (Burkitt, 1975; Gaulin and Konner, 1977). Thus, the usefulness of rank-ordering food types along a unitary dimension of quality may be limited. On the basis of these results, however, Demment's (1983) argument concerning fibre levels in male and female diets can be questioned, and in Chapter 6 I re-examine his hypothesis using data from the current study.

(b) Relationship between food quality and abundance

It is often suggested that an inverse relationship exists between the nutritive value of potential food items and their abundance (Jarman, 1968; Bell, 1971; Demment, 1983: Demment and van Soest 1985). Thus the fibrous structural tissue of plants (i.e. woody stems) comprises a large proportion of the biomass, particularly in densely wooded or forested areas, photosynthetic parts rather less, and reproductive and storage organs least of all. Because energy is lost from ecological systems at each successive higher trophic level (Odum, 1968; Whittaker, 1975) animal matter, generally considered the highest quality, lowest fibre item available to primates (e.g Sailer *et al.*, 1985) will be less abundant than plant matter. It is this inverse relationship between abundance and quality, coupled with the negative allometry of metabolic rate, that has been given as the explanation for observed relationships between body size and diet (Jarman, 1968; Bell, 1971; Clutton-Brock and Harvey, 1977a,b; Gaulin, 1979; Sailer *et al.*, 1985); small-bodied species have high mass-specific metabolic rates but lower overall requirements, so are expected to concentrate on high-quality resources which are relatively rare. Larger species have higher total requirements, so should eat relatively low-quality but abundant foods.

Demment (1983; Demment and van Soest, 1985) extends these arguments to predict sex differences in the feeding of male and female baboons; as noted in the previous section, males are expected to have relatively high-fibre diets, because digestive efficiency relative to metabolic requirements

increases with body size, while high-fibre items are thought to be commonest amongst the available foods.

In order to test the hypothesis that a relationship exists between abundance and quality of food items, I have calculated correlations between mean monthly biomass and phytochemical measures for the food classes listed in Table 5.1. None of these are significant (Protein; $r=0.085$, $p=0.369$: Fibre;$r=^{-}0.075$, $p=0.384$: Condensed tannins; $r=^{-}0.254$, $p=0.154$: Protein/(ADF+condensed tannins); $r=^{-}0.067$, $p=0.395$).

These results may seem a little surprising, but it is important to bear in mind that the correlations pertain specifically to the range of items eaten by the baboons, not to plant matter within the environment more generally. As Demment and van Soest (1985) argue, his curve of crude fibre content against biomass (p.648) may have relevance for understanding differences between herbivores of greatly different size, but application to the intraspecific situation depends on the relationship holding good across the relatively small part of the curve within which baboon foods fall. Interpolation into Demment and van Soest's fibre curve of the ADF values obtained for baboon foods here reveals that those foods occupy only the low-fibre end (<50%), over which the relationship with biomass appears to be weak or absent. This is basically because baboons do not eat tree trunks and branches, or other excessively fibrous and abundant material. The scale of the ecological relationship represented by Demment and van Soest's fibre curve is too broad to be readily applied to the intraspecific situation.

Some high-quality (low-fibre) foods are nevertheless obviously relatively scarce and/or hard to process. Examples include the individual seed kernels of *Acacia* trees, and animal matter. The latter did not enter into the correlations above, because biomass estimates were not available, but there seems little reason for doubting that it is comparatively rare, and it is undoubtedly high in protein and low in fibre (Hladik, 1977; Gaulin and Konner, 1977). It is possible, then, that females concentrate on such foods more than males do, and the question of differences in diet quality is pursued in Chapter 6.

3. DIET

a) Dietary diversity

During the twelve month study-period, the baboons were observed to eat 108 foods from 76 plant species (72 identified to genus, 64 to species). In addition, 7 vertebrates and various unidentified invertebrates were eaten. These foods are listed in Appendix II.

TABLE 5.5: SUMMARY OF FOOD SPECIES DIVERSITY IN SEVEN STUDIES OF *PAPIO* BABOONS.

	% time on top 2spp.	% time on top 5spp.	Total number of species	Rainfall	Months
P.anubis[1]	26.2	41.6	76	580 mm	10
P.cynocephalus[2]	50.0	>60.0	30	300 mm	11
P.cynocephalus[3]	n.a	n.a.	180	842 mm	60
P.ursinus[4]	33.4	63.1*	n.a.	457 mm	?
P.papio[5]	23.5	45.4	58	1000 mm	12

1 This study; 2 Post (1978); 3 Norton *et al.* (1987); 4 Hamilton *et al.* (1978); 5 Sharman (1981).

In Table 5.5, data from this and other studies on the percentage of time spent feeding on the top 2 and top 5 food species, and on the total number of species utilised are presented. Dietary diversity must be at least partly a function of study duration and the amount of observation time, but three studies - this one, and those by Post and by Sharman - were of approximately equal duration (10-12 months), so enable valid comparisons. In terms of the percentages of time spent feeding on the top two and top five species, the results from the present study and those from Sharman's study of *P.papio* in Senegal are very similar. The total number of species utilised are also not too dissimilar. In contrast, the results obtained by Post for *P.cynocephalus* in Kenya indicate considerably lower diversity; greater percentages of feeding time were spent on the most favoured species, and the total number utilised was only 30. The most likely explanation is that the Amboseli habitat is relatively depauperate; rainfall was only 300 mm, at the bottom end of the range for semi-arid savannah (Delaney and Happold, 1975), and, prior to Post's study, the habitat had been transforming into a halophytic, xeromorphic one (Post, 1978). In their five-year study of diet in *P.cynocephalus* at Mikumi, Tanzania, Norton *et al.* (1987) observed the utilisation of 180 species, and argued that this great diversity was due to habitat richness as well as to the long duration of their study. Unfortunately they did not provide the data to test this hypothesis, but they did estimate that about 700 plant species were available, and rainfall at Mikumi is relatively high (842 mm.).

Dietary diversity can be quantified using the Shannon-Weiner index (Harvey, 1977; Oates, 1977; Post, 1977). This is calculated as

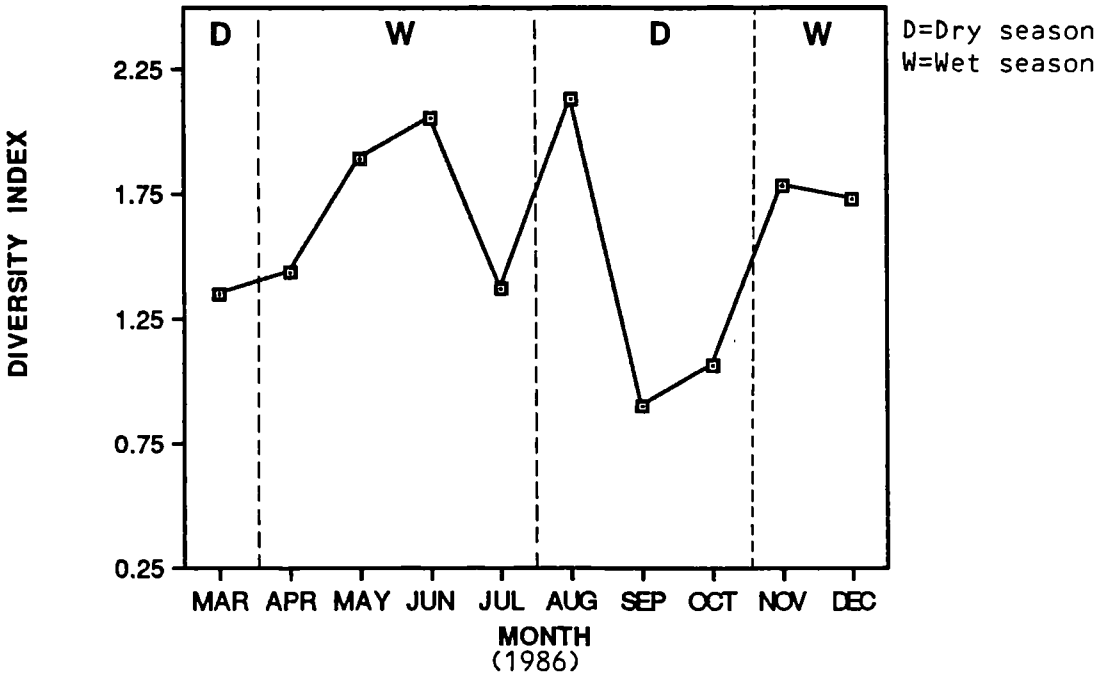
$$H = -\Sigma\ p_i\ (\log_e\ p_i)$$

where p_i is the proportion of time spent feeding on each food type. I have calculated dietary diversity according to this index, using the proportions of dry weight intake made up by each of the major food types; intake, rather than feeding time is considered more appropriate, because it reflects nutrition more closely, but, in this case, it makes no difference to the overall conclusions. Post (1978) used the same index, but, as he notes, comparisons between studies is problematic because the value of the index depends on the way in which foods are classified; clearly, the grosser the classification, the lower the apparent diversity will tend to be. So the fact that the mean value of 1.848 obtained by him (calculated from his Table 24) is greater than the 1.55 obtained in the present study probably reflects the fact that he used 24 food categories, whereas I used only 16 in this analysis. This is illustrated by the fact that calculation of the index across all food species and parts, without pooling data into categories, yields the markedly higher figure of 2.69.

b) Seasonal variation in dietary diversity

Variation in the diversity index during the ten-month period is plotted in Figure 5.1. Diversity tended to be higher in wet season months (mean=1.71) than in dry season months

FIGURE 5.1: MONTHLY VARIATION IN DIETARY DIVERSITY (SHANNON-WEINER INDEX)



(mean=1.36), but this difference was not significant (t=1.1, df=3, p=0.32). Post (1978) found that diversity was non-significantly correlated with monthly rainfall, but significantly with rainfall for the previous month. Correlations with rainfall and food biomass in the present study are presented in Table 5.6: all are in the expected direction (positive), and the coefficients for rainfall in preceding months is higher than that for the same month; none, however, are significant.

TABLE 5.6: CORRELATIONS BETWEEN DIETARY DIVERSITY AND FOOD BIOMASS AND RAINFALL

	r	n	p
FOOD BIOMASS	0.433	8	0.284
RAINFALL			
SAME MONTH	0.380	10	0.279
PREVIOUS MONTH	0.467	10	0.174
SAME + PREVIOUS	0.488	10	0.151
SAME + TWO PREVIOUS	0.508	10	0.134

The results of this analysis are suggestive, but not conclusive; there is some indication that rainfall has an effect on dietary diversity, but the pattern is not completely clear. The low diversity of the diet in July, towards the end of the wet season, reflects the intensive utilisation of herb fruits and grass seeds, which together made up 79.4% of the diet at that time (section 5.2.f). In the following month, availability of these foods had declined (Figure 3.6), and dietary diversity increased. The situation appears to be a complex one, and the causal relationships are not clear. On the other hand, the sample size is small, and, as noted, Post did obtain significant correlations.

c) Effects of gender and reproductive state on diversity

Individual differences in foraging behaviour and dietary profile may reflect variation in biological constraints (Clutton-Brock, 1977; Demment, 1983), variation in competence (Whiten, 1988), competitive exclusion (e.g. Wrangham, 1980; Dittus, 1979; Post et al. 1980; Van Schaik, 1987), or all three. This topic is pursued with respect to nutrient intakes and troop spatial organisation in Chapters 6 and 7. Diversity, however, is also a relevant parameter - Post (1978, Table 29) found that the diets of adult females were less diverse than those of adult males. His sample, however, consisted of only four individuals. Here I extend his analysis, using my larger sample of 19 females and seven males, and also examine the implications of females' reproductive states.

Comparison of average diversity indices for males and females in each study month indicates no significant difference ($t=-0.08$, $df=6$, $p=0.936$). It is possible, however, that variation exists within the female sample due to the constraints of different reproductive states. Perhaps surprisingly, there is a positive correlation between the number of months spent cycling by females and their mean diversity indices ($r=0.420$, $df=17$, $p=0.037$), indicating that females' diets are less diverse when they are pregnant and/or lactating. The mean monthly diversity indices are 1.811 for cycling females, 1.732 for lactating females, 1.593 for pregnant females, and 1.590 for males. Thus, far from females having less diverse diets

than males, as in Post's (1978) study, their diets were if anything *more* diverse. The differences amongst these groups are not, however, statistically significant overall ($F=0.688$, $df=3,28$, $p=0.567$). Examining the picture within individual months, cycling females had more diverse diets than pregnant females in 7 out of 8 months, and more diverse diets than lactating females, also in 7 out of 8 months, but more diverse diets than males in only 5 months. Likewise, male diets were more diverse than those of pregnant and lactating females in 5 out of 8 months. The differences amongst the groups were significant in only two (July: $F=4.233$, $df=3,23$, $p=0.019$; September: $F=3.865$, $df=3,20$, $p=0.025$). Post hoc tests reveal that the values for cycling females were significantly higher than those for pregnant females (Tukey test; $Q=4.272$, $p=0.031$) in July, and significantly higher than those for males in September (Tukey test; $Q=5.181$, $p=0.017$). Experimentwise error rates (e.g. Harris, 1975) are a potential problem here, since, given n repeated tests of a hypothesis, one would expect $n(0.05)$ significant results on a random basis (assuming the usual significance value of 5%). In the present case $8(0.05)=0.4$ significant results expected by chance, compared to the two actually obtained, so it looks as though the trends, though weak, are real.

Why might pregnant and lactating females have less diverse diets than cycling females? One explanation is that they may be more constrained in their diet selection because of a need to avoid toxic secondary compounds capable of damaging the foetus or the suckling infant (Janzen, 1978). This hypothesis

is evaluated with respect to the alkaloid intake of females in Chapter 6.

It is difficult to suggest plausible reasons for the lack of agreement between this study and Post's (1978) findings, as regards an overall sex difference in dietary diversity. As noted, however, Post collected data on only two individuals of each sex. In addition, the females were pregnant or lactating for 73% of the study period, but the possible influence of reproductive state was not taken into account.

(d) Relationship between dominance and dietary diversity amongst adult females

If high-ranking females dominate access to preferred foods, low-ranking females might be forced to expand their diet to include other, more marginal foods (suggested by Hamilton *et al.*, 1978); under these conditions we would expect a negative correlation between dominance and diversity. On the other hand, high-ranking females might exclude low-rankers specifically from rarely-encountered "special" foods, suggesting, perhaps, a positive correlation between rank and diversity (suggested by Post, 1978). There are therefore no strong theoretical reasons for making a prediction one way rather than another.

In fact, there is no significant correlation between females' dominance ranks and their average dietary diversity ($r=0.139$, $df=17$, $p=0.572$). This is also true within each of the eight main study months (May, $r_s=0.009$; June, $r_s=0.158$; July,

r_s=0.039; August, r_s=⁻0.141; September, r_s=⁻0.059; October, r_s=0.241; November, r_s=0.038; December, r_s=0.094 - all p>0.05 with df=16-17). It is possible that a real relationship is being obscured by the confounding effect of reproductive state. In order to test this, I regressed mean diversity on the number of months spent cycling, and correlated the residual values from the regression with dominance rank; the correlation is not significant (r_s=⁻0.170, df=19, p=0.486).

e) Annual composition

In Table 5.7 information is presented on the utilisation of the top 30 foods, in terms of both percentage of dry weight intake and percentage of feeding time (means of results for 10 months, March-December inclusive). Although the two types of measure are well correlated overall (r=0.858, df=187, p<0.001) there are a few important differences. For example, the fleshy stems of *Euphorbia nyikae* ranked third in terms of dry weight intake, at 7.92%, but only eighth, with 3.82%, in terms of feeding time. Conversely, corms of the sedge *Cyperus blysmoides* ranked only thirtieth on dry weight intake (0.53%), but tenth in terms of feeding time, providing confirmation for Post's suspicion that the large amount of time devoted to corm harvesting by *P.cynocephalus* at Amboseli overestimated actual intake. Here, time spent feeding also considerably overestimates intake for the bulbs of *Mariscus amauropus*. Little would be gained by multiplying examples; suffice to say that, as noted by Konner and Gaulin (1977), percentage time, the usual measure in primate ecology, will not always

TABLE 5.7: PERCENTAGE OF TIME SPENT FEEDING ON TOP 30 FOODS

	% feeding time	cumulative %
Acacia etbaica flowers	12.56	12.56
Marsicus amauropus bulbs	9.65	22.21
Tribulus terrestris achenes	7.98	30.19
Lycium europaeum leaves	5.78	35.97
Cynodon plectostachyus foliage*	5.63	41.60
Acacia tortilis flowers	4.83	46.43
Tragus bertorianus flowers	4.93	51.36
Euphorbia nyikae fleshy stems	3.82	55.18
Acacia etbaica dry seeds	2.98	58.16
Cyperus blysmoides corms	2.86	61.02
Penissetum spp. foliage*	2.78	63.80
Cynodon dactylon foliage*	2.28	66.08
Acacia mellifera fresh pods	1.88	67.96
Trachyandra saltii leaves	1.78	69.74
Osteospermum vailantii capsules	1.74	71.48
Acacia seyal fresh seed kernels	1.45	72.93
Tribulus terrestris leaves	1.41	74.34
Euphorbia spp. fleshy stems	1.39	75.73
Sansevieria intermedia bulbs	1.19	76.92
Ipomoea mombassana achenes	1.09	78.01
Kyllinga nervosa bulbs	1.06	79.07
Commelina erecta flower buds	1.04	80.11
Cyperus merkeri bulbs	1.04	81.15
Acacia etbaica fresh pods	1.02	82.17
Polichia campestris berries	1.01	83.18
Acacia tortilis seed kernels	0.90	84.08
Acacia mellifera flowers	0.88	84.96
Asparagus africanus leaves	0.87	85.83
Oxygonum sinuatum leaves	0.79	86.63
Acacia mellifera exudate	0.78	87.41

* Blades and meristems

TABLE 5.8: PERCENTAGE OF DRY WEIGHT INTAKE MADE UP BY TOP 30 FOODS

	% INTAKE	CUMULATIVE %
Acacia etbaica flowers	15.58	15.58
Cynodon plectostachyus foliage*	9.25	24.83
Euphorbia nyikae fleshy stems	7.92	32.75
Tribulus terrestris achenes	5.67	38.42
Acacia mellifera fresh pods	5.48	43.90
Tragus bertorianus flowers	5.34	49.24
Acacia tortilis flowers	5.27	54.51
Cynodon dactylon foliage*	4.68	59.19
Penissetum spp. foliage*	4.25	63.44
Lycium europaeum leaves	3.55	66.99
Tribulus terrestris leaves	3.35	70.34
Trachyandra saltii leaves	2.64	72.98
Mariscus amauropus bulbs	2.43	75.41
Acacia etbaica dry seeds	1.97	77.38
Osteospermum vaillantii capsules	1.56	78.94
Solanum incanum green fruits	1.47	80.41
Acacia brevispica fresh pods	1.46	81.87
Euphorbia spp. fleshy stems	1.37	83.24
Acacia mellifera flowers	1.15	84.39
Pelargonium quinguelobatum roots	1.12	85.51
Cyperus merkeri bulbs	0.76	86.27
Acacia brevispica leaves	0.72	86.99
Sansevieria intermedia bulbs	0.72	87.71
Acacia seyal fresh seed kernels	0.70	88.41
Ipomoea mombassana achenes	0.63	89.04
Kyllinga nervosa bulbs	0.63	89.67
Asparagus africanus leaves	0.58	90.25
Acacia mellifera dry seeds	0.58	90.83
Ipomoea obscura achenes	0.56	91.39
Cyperus blysmoides corms	0.53	91.92

* Blades and meristems

accurately reflect actual intake. The different measures will be appropriate for different types of analysis; percentage time will be most appropriate where the concern is with time-budgeting, such as in the explanation of variation in habitat preferences (Chapter 3), whereas percentage intake is more useful when considering nutrition and diet selection (this chapter, and Chapter 6).

The percentages of dry weight intake and of time spent feeding for the major food classes are presented in Table 5.9. Several features of the dietary breakdown deserve attention.

(i) Underground items The percentage of feeding time on underground items, at 15%, is quite low in comparison to populations of *Papio* baboons studied elsewhere; data collated by Dunbar (1988 - Table 13.2), with additions from Norton *et al.* (1987) and from the present study, indicate a range from 1.4% (*P.anubis* at Bole, Ethiopia) to 53.4% (*P.ursinus* in the Drakensberg mountains, South Africa), with a mean of 23.4% (Table 5.10). The percentage of the diet made up of grass and sedge corms is considerably lower in the present study (even when sedge bulbs are included - see section 5.1(a)) than in Post's (1978) study, in which subjects spent over 30% of their feeding time on this item. Mention has already been made of the low rainfall and relatively depauperate nature of the habitat at Amboseli, and subterranean foods are thought by some researchers to constitute a "fall-back", or "bottleneck"

TABLE 5.9: PERCENTAGE OF TIME SPENT FEEDING AND OF DRY WEIGHT INTAKE FOR MAJOR FOOD CLASSES.

FOOD	Mean of monthly percentage % Time	% Dry weight
Sedge bulbs	11.37 (8.00)	4.31 (3.68)
Sedge corms	2.86 (3.19)	0.97 (1.44)
Roots	0.96 (1.17)	1.47 (1.97)
Grass foliage	13.99 (13.06)	19.96 (15.47)
Other foliage	12.84 (9.81)	12.43 (11.91)
Acacia flowers	18.01 (27.94)	22.00 (31.56)
Grass flowers/seedheads	8.92 (9.80)	5.82 (11.74)
Other flowers	2.56 (2.97)	0.87 (1.27)
Acacia seeds/pods	8.92 (8.98)	9.66 (10.39)
Berries	1.93 (2.77)	1.99 (2.61)
Dry fruits	11.66 (15.65)	9.48 (12.32)
Succulents	5.21 (8.40)	9.29 (12.50)
Animal	0.95 (1.84)	0.67 (1.13)

Notes: Figures in brackets are standard deviations

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food when availability of preferred items is low (Post, 1978; Whiten *et al.*, 1987); although in some cases they may be quite high quality (see Table 5.1), the time and energy costs of digging are likely to be high. Rainfall data for most of the study sites listed in Dunbar (1987) are available from Sharman and Dunbar (1982). Adding data from the present study, and from the study by Norton *et al.* (1987) the correlation between mean annual rainfall and percentage of the diet made up by underground items is actually positive and not significant ($r=0.182$, $df=9$, $p=0.592$). The Drakensberg site of Whiten *et al.* (1987) is, however atypical. It is a montane, rather than a savannah habitat, with high rainfall, but low productivity; baboon food biomass, assessed using similar methodology to my own, varied between only 0.552 - 0.800 g/m^2, compared to the mean of 3.51g/m^2 in the present study. The rainfall figure listed by Sharman and Dunbar for Ruaha is somewhat anomalous; it is given as 1680 mm, and, while Ruaha is described as being "comparatively open....savannah" (Collins, 1984), 1600mm is

the approximate isohyet marking the transition from savannah to forest (Delaney and Happold, 1975). When these two sites are removed from the analysis, we find a significant negative correlation between rainfall and utilisation of underground items ($r=-0.699$, $df=7$, $p=0.036$). If it is assumed that food availability is lower in drier habitats, this provides some confirmation for the idea that in general they represent a sub-optimal food class relative to above-ground items.

TABLE 5.10: RAINFALL AND DIET OF BABOON POPULATIONS

		PERCENTAGE OF TIME FEEDING ON				
	RAIN*	UNDERGROUND	FRUITS	FLOWERS	LEAVES	ANIMALS
1.	580	15.0	23.2	21.0	27.3	0.9
2.	1105	1.5	40.8	11.7	41.1	3.9
3.	690	27.0	9.5	2.6	52.9	1.9
4.	1380	6.6	48.6	2.2	13.9	13.1
5.	300	32.5	27.1	4.7	15.2	0.6
6.	1680	51.6	15.5	1.4	18.7	8.7
7.	842	11.7	42.6	20.3	13.9	?
8.	700	39.0	43.3	7.3	8.0	2.6
9.	631	16.0	42.0	12.0	25.0	2.5
10.	1197	53.4	2.5	14.3	25.7	3.9
11.	941	3.1	73.5	8.6	8.5	1.4
MEAN	913	23.4	33.5	9.6	22.7	3.9
S.D.	399	18.6	20.4	6.9	13.9	4.0

Notes: * mean annual rainfall (mm).
Papio anubis; 1. Present study; 2. Bole, Ethiopia; 3. Gilgil, Kenya; 4. Gombe, Tanzania. ***Papio cynocephalus***; 5. Amboseli, Kenya; 6. Ruaha, Tanzania; 7. Mikumi, Tanzania. ***Papio ursinus***; 8. Suikerbosrand, S.Africa; 9. Cape Reserve, S.Africa; 10. Drakensberg, S.Africa. ***Papio papio***; 11. Mt. Assirik, Senegal

(ii) Fruit Most of the fruit consumption by the baboons involved dry and fibrous varieties rather than berries. Of the latter, most were unripe fruits of *Solanum incanum*, which is not sweet, but extremely "bitter and inedible, and is more or less poisonous" (Watt and Breyer-Brandwijk, 1962). Post

(1978) lists it as a common plant avoided by baboons at Amboseli. Altmann and Altmann (1970, p.148) mention that it was eaten for a short time during their initial study there, although, curiously, Altmann (1982) later refers to it as "deadly and rejected". The genus *Solanum* is generally characterised by the bitter gluco-alkaloid solanine (Watt and Breyer-Brandwijk, 1962; Waterman,1985), and the alkaloid assay used here did give positive results for both ripe and unripe fruit, though less strongly so in the case of the latter (Table 5.3). The significance of the utilisation of this plant is discussed in relation to alkaloid content in section 5.3.b(ii).

The only sweet-tasting berries eaten in significant quantities were those of *Polichia campestris* and *Grewia tembensis*, together making up 1.4% of feeding time and 0.9% of dry weight intake. This lack of sweet, fleshy fruits in the diet is most likely to have been due to their scarcity, rather than to their not being a preferred item; when the baboons encountered them, they fed avidly on them, and this is reflected in high selection ratios (mean=4.13 - see section 5.3). Similar observations have been made on baboons at other study sites (Altmann and Altmann, 1970; Hamilton *et al.*, 1978), so there seems some justification for the idea that, as a genus, they do exhibit a tendency to frugivory (Dunbar, 1988). It is then availability which determines the expression of this tendency in terms of the composition of the diet. Since availability is probably often fairly low (Post, 1981; this study), diet composition data may not suggest that frugivory is a characteristic of baboons, at least once the proper

distinctions have been made between types of fruit. Confusion could perhaps be avoided by making a clear distinction between dietary preferences and dietary composition. At the moment, for baboons, we have quite a lot of information on the latter, but very little on the former.

Across populations there is no correlation between rainfall and the proportion of fruit and seeds in the diet ($r=^{-}0.067$, df=9, p=0.844). The correlation improves, but remains non-significant, when the two aberrant populations are removed (r=0.503, df=7, p=0.168). The lack of correlation is none too surprising, given the pooling of all types of fruit and seeds. Possibly the most relevant environmental determinant of fruit consumption would be tree cover, because this can be expected to influence availability both of grasses (negatively) and of large, fleshy tree fruits (positively) - c.f Whiten *et al.* (1987, p.383). To the extent that rainfall determines tree cover, then, it may affect the proportion of berries and drupes in the diet; perhaps this goes some way towards explaining the high figure of 73.5% and 48.6% fruit at Mt. Assirik and Gombe respectively, both of which had relatively dense tree cover.

(iii) Flowers Since trees potentially yield large numbers of flowers, the proportion of flowers in the diet might also be expected to correlate with tree coverage, and therefore, by proxy, rainfall. Once again, however, there is no correlation with rainfall ($r=^{-}0.298$, df= 9, p=0.372; with Drakensberg and Ruaha removed, $r=^{-}0.159$, df=7, p=0.682). The greatest degree of florivory of all the populations in Table 5.10 was found

in the present study, but of the 21% total, the great majority was comprised by *Acacia* flowers (18%) whereas, in at least three of the other studies in Table 5.10 , this was not the case (Sharman, 1981; Whiten, *et al.*, 1987; Norton *et al.*, 1987).

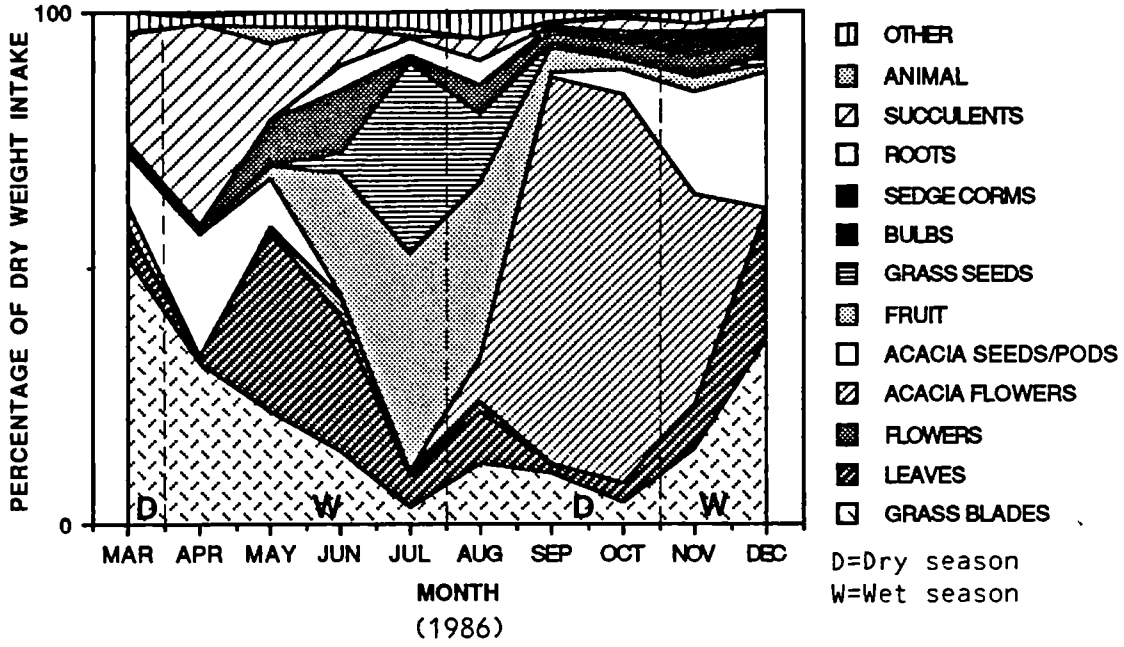
(iv) Foliage Leafy matter made up about 27% of the diet, as time spent feeding, or 32% of dry weight intake, well below the 53% recorded by Harding (1976) at Gilgil, but slightly above the mean for all the populations in Table 5.10. There is no correlation with rainfall ($r=^{-}0.067$, df=9, p=0.844), even with the two "aberrant" populations removed ($r=^{-}0.035$, df=7, p=0.913). Once again, to the extent that tree cover is determined by rainfall, we might expect to find a negative correlation with grass blade consumption, and a positive correlation with tree leaf consumption, when these two are differentiated, and, indeed, the former relationship was demonstrated by Dunbar (1984b).

(v) Succulents One important food class in the present study was that of succulents (5% of feeding time, and 9% of intake). Principally this involved two spurges; *Euphorbia nyikae* (a tree-sized plant from which the baboons broke off large segments of the fleshy stem nodes), and an unidentified *Euphorbia* (a small, herb-sized plant, possibly *E.heterochroma*, from which the sharp spines were removed with hands and teeth before consumption of the finger-like stems). Both of these contained latex, which is reputed to be poisonous (Watt and Breyer-Brandwijk, 1962), and which was observed to flow copiously from the broken stumps after the baboons had fed.

Similar observations have been made by Lock (1972), for *Papio anubis* feeding on *E.candelabrum* (another tree-like species) in Uganda, and for *P.cynoceohalus* by Norton *et al.* (1987), but no previous study has reported such intensive utilisation. In the very dry period January-February 1986, before I had begun collecting detailed data, *E.nyikae* appeared to be the single most important component of the diet, with the possible exception of dry *Acacia* seeds picked from the ground. It may therefore be a "bottleneck" food, perhaps functionally akin to corms at Amboseli (Post, 1981). Apart from the latex, which is reputed to be quite toxic to some animals (Watt and Breyer-Brandwijk, 1962), these plants contain little protein, but much water, especially in comparison to other major dry season foods, such as *Acacia* flowers and dry seeds (Table 5.1). It grew mainly in the drier, eastern half of the home range, where no permanent standing water was available, so it may have provided an important water source when the baboons travelled in this area during the dry season (against this it must be said that the baboons also got water by digging in the dried-out sandy beds of gullies).

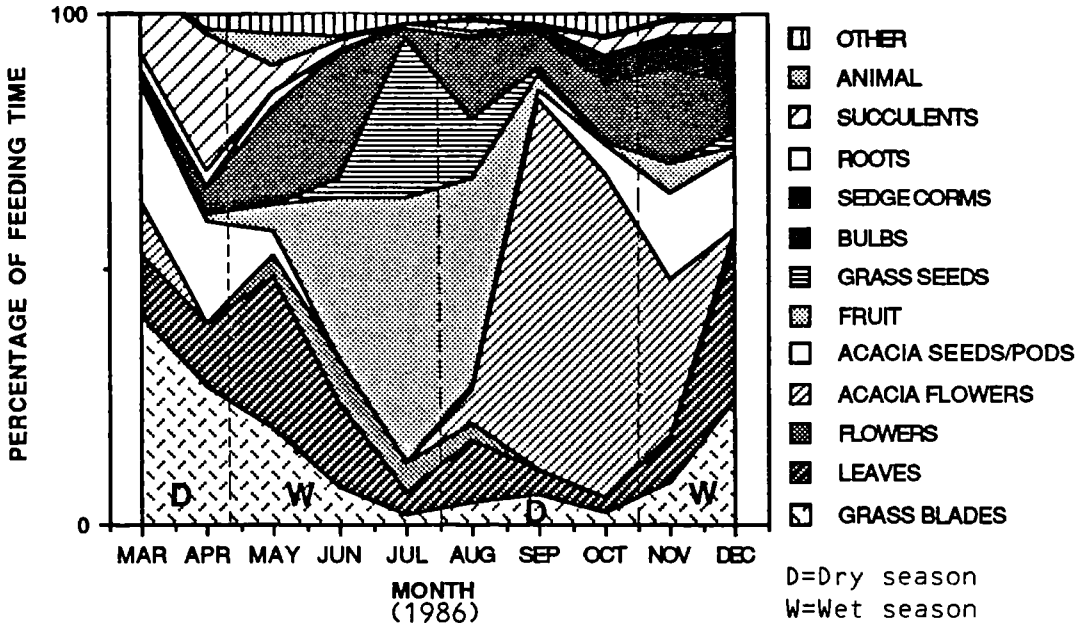
(vi) Animal matter Consumption of animal matter was relatively low in the present study (0.9% of feeding time, compared to the mean of 3.9% in Table 5.10). Across populations, rainfall is positively correlated with the proportion of the diet comprised of animal matter ($r=0.804$, $df=9$, $p=0.006$; with Drakensberg and Ruaha removed, $r=0.815$, $df=7$, $p=0.014$). The relationship is perhaps against expectations, since rates of predation by baboons generally increase during the dry season (Dunbar, 1984b; Strum, 1981).

FIGURE 5.2: MONTHLY VARIATION IN DIET COMPOSITION (INTAKE)



Area graph diplaying percentage of dry weight intake made up by major food types in each month.

FIGURE 5.3: MONTHLY VARIATION IN DIET COMPOSITION (FEEDING TIME)



Area graph displaying percentage of feeding time on major food types in each month.

The latter results, however, concern vertebrate prey, whereas the major proportion of the values in Table 5.10 may represent invertebrates; vertebrates made up only 0.01% of the 0.9% total for Chololo. Many invertebrates, such as caterpillars, are likely to be more abundant in wet conditions, because they depend directly on the availability of green vegetation for food. In turn, invertebrate predators, such as scorpions, which were also eaten by the baboons in the present study, will depend on the availability of herbivorous invertebrates. This also suggests a seasonal pattern related to rainfall, and this is indeed evident (see below).

One final comment on the subject of overall diet composition is necessary. Results in the present study are based on observations over a period of less than a year (ten months), and most of the studies in Table 5.11 were of roughly similar duration. The study by Norton *et al.* (1987), however, is an exception which raises a question about the validity of characterising baboon diets on the basis of these relatively short observation periods. Norton *et al.* present data for a five-year period, arguing that had they been restricted to a single annual cycle they would have gained a rather misleading picture of long-term dietary composition. Thus, one dry season or one wet season is not necessarily like another. This is probably more true of baboons than of other primates, because of the flexible nature of their ecological niche and the breadth of their diet. We therefore need to exercise a certain amount of caution in the weight we give to the details of dietary profiles derived from shorter-term studies. In the

present case, the population concerned appears to be unusual in the lack of reliance on corms, but consumption of this item was more substantial in the following year (Lochhead, pers. comm.). Elucidation of the principles underlying these long-term fluctuations will be a task for future research.

c) Monthly variation in diet composition

Figures 5.2 and 5.3 show monthly variation in the proportions of time spent feeding and of dry weight intake for the major food classes. Table 5.11 shows that, in general, variation

TABLE 5.11: CORRELATIONS BETWEEN BIOMASS AND PROPORTION OF DRY WEIGHT INTAKE FOR MAJOR FOOD TYPES

FOOD TYPE	r	p (1-tailed)
Grass blades	0.618	0.050
Herb leaves	0.765	0.013
Shrub leaves	0.832	0.005
Acacia leaves	0.005	0.495
Sedge bulbs	0.065	0.439
Grass flowers/seeds	0.815	0.007
Herb flowers	0.897	0.001
Acacia flowers	0.896	0.001
Herb fruits	0.641	0.044
Acacia pods	0.629	0.047
Acacia dry seeds	0.719	0.022

for each category was positively correlated with variation in its availability (dry weight biomass). The two exceptions are sedge bulbs and *Acacia* leaves. In both of these there are problems associated with sampling error. Sedge bulb

availability was evaluated on the basis of what was visible *above* ground, though this is inevitably a problematic procedure. Alternatively, the lack of correlation might indicate that sedge bulbs were not eaten in accordance with their availability, but were used as a low-quality fall-back food when general food availability was low. If this were the case we would expect a negative correlation between overall food biomass and the proportion of the diet made up by sedge bulbs; in fact the correlation is positive, but not significant ($r=0.597$, $df=8$, $p=0.118$; controlling for effect of sedge bulb availability, partial $r=0.595$, $df=7$, $p=0.160$). *Acacia* leaves are represented by only one species, *A.brevispica*, which was relatively uncommon, and therefore not sampled very adequately for the purposes of this analysis.

In Chapter 3 it was shown that the availability of certain foods, notably the various types of foliage, was positively correlated with rainfall. Given that availability is a **proximal** influence on consumption, we would therefore expect rainfall to emerge as the **distal** cause of seasonal variation in dietary profiles. Correlations between rainfall and the proportion of dry weight intake made up by each food type are presented in Table 5.12. A problem with these analyses is that the probability of obtaining "significant" results by chance increases in direct relation to the number of tests carried out. Since a large number of correlation coefficients are presented in Table 5.12, there is a correspondingly high chance of erroneously rejecting the general null hypothesis that rainfall has some effect on intake of some foods. The expected rate of making such errors (known as the

TABLE 5.12: CORRELATIONS BETWEEN RAINFALL AND PERCENTAGE CONTRIBUTION TO THE DIET

	Grass blades		Herb leaves		Shrub leaves	
	r	p	r	p	r	p
Same month	0.238	0.508	0.490	0.150	-0.174	0.630
Previous	0.659	0.045*	0.756	0.012*	0.170	0.636
Same+previous	-0.036	0.922	0.721	0.018*	0.003	0.992
Same+2 previous	-0.267	0.456	0.566	0.088	0.292	0.443

	Tree leaves		Grass flowers		Herb flowers	
	r	p	r	p	r	p
Same month	-0.071	0.846	-0.137	0.706	0.268	0.454
Previous	0.163	0.652	0.470	0.170	0.544	0.104
Same+previous	0.057	0.876	0.203	0.584	0.473	0.168
Same+2 previous	-0.162	0.652	0.847	0.002**	0.793	0.006**

	Acacia flowers		Herb fruits		Shrub fruits	
	r	p	r	p	r	p
Same month	-0.564	0.090	0.018	0.960	-0.338	0.340
Previous	-0.548	0.100	0.573	0.084	-0.032	0.913
Same+previous	-0.640	0.046*	0.350	0.322	0.207	0.548
Same+2 previous	-0.436	0.208	0.809	0.004**	0.329	0.354

	Acacia pods[1]		Acacia seeds[2]		Succulents	
	r	p	r	p	r	p
Same month	0.016	0.966	0.491	0.150	0.681	0.030*
Previous	-0.159	0.660	-0.344	0.330	-0.067	0.854
Same+previous	-0.087	0.810	0.071	0.846	0.341	0.336
Same+2previous	-0.584	0.076	-0.698	0.024*	-0.267	0.456

	Sedge bulbs		Sedge corms		Roots	
	r	p	r	p	r	p
Same month	0.392	0.164	-0.552	0.098	0.022	0.950
Previous	0.547	0.102	-0.361	0.306	0.403	0.248
Same+previous	0.542	0.106	-0.344	0.330	0.252	0.482
Same+2previous	0.604	0.064	-0.438	0.206	0.759	0.010**

	Animal matter	
	r	p
Same month	0.469	0.172
Previous	0.663	0.036*
Same+previous	0.655	0.040*
Same+2previous	0.383	0.272

Notes: [1] Dehiscent pods eaten whole [2] Seeds extracted from pods

experimentwise error rate - see section 2(c) above) is equal 60(0.05)=3; we would expect 3 "significant" results by chance, whereas there are in fact 12. Likewise, at p=0.01 we would expect 60(0.01)=0.6 results, in contrast to the 5 obtained. It therefore seems reasonable to conclude that rainfall patterns did indeed influence dietary composition.

As expected, consumption of at least some classes of foliage (grass blades and herb leaves) was generally positively correlated with rainfall, in the case of grass blades, with rainfall for the same month, and in the case of herb leaves, most strongly with rainfall in the previous month. These results correspond with those obtained by Post (1978).

Reproductive parts not surprisingly showed more of a time lag in getting into the diet, reflecting the fact that foliage tends to be produced first, with flowers and fruits emerging later (see Table 3.2); thus consumption of herb flowers and herb fruits correlated most strongly with rainfall for the previous two months. Consumption of dry *Acacia* seeds picked up from the ground, and of *Acacia* flowers, however, correlated **negatively** with rainfall (in the previous two months and in the previous month, respectively). Consumption of fresh pods and seeds was uncorrelated with rainfall.

For practical reasons, monthly variation in the biomass of succulents, roots, sedge corms and invertebrates was not measured. Consumption of succulents correlated positively with rainfall for the same month, rather going against the

idea that they are utilised principally as a dry season food. The proportion of dry weight intake made up by roots was also positively correlated with rainfall in the two previous months, possibly because it is easier to find them and pull them up once green growth has appeared above ground. Not all underground items, therefore, can be considered dry season fall-back foods. Sedge corms, by contrast, do seem to fill this role, consumption being negatively correlated with rainfall. As Post (1978) has pointed out, however, corms are probably also less nutritious in the wet season (since nutrients are transferred into stem and leaf growth at this time) so variation in food value may contribute to the seasonal patterns observed. Finally, consumption of invertebrate prey was positively correlated with rainfall (previous month and same+previous month), replicating the findings of Sharman (1981). This seasonal pattern mirrors the association between annual rainfall and time spent feeding on animal matter by different populations of baboons, supporting the idea that prey availability is higher in relatively wet conditions.

The absence of significant correlations in the cases of some food types does not mean that no relationship with rainfall exists; it is highly likely that both availability and consumption are ultimately linked to rainfall patterns for all food types (as well as to inter- and intraspecific competition - Strum and Western, 1982). The difficulty lies in establishing the exact nature of the relationship between temporal patterns of rainfall and the responses of different kinds of plants. Trees obviously tend to respond more slowly

than do grasses and herbs, for example. Elucidation of these longer-term phenological patterns must await data collected over a period of years, rather than months.

4. PHYTOCHEMICAL DETERMINANTS OF DIETARY PREFERENCES

In a review of the literature on primate feeding selectivity in relation to plant chemistry, Waterman (1984) stated that

> "Selection appears to correlate with both positive and negative factors in leaves, with protein being the most significant nutrient. The same is probably true for flowers and perhaps for seeds. In fruits, other nutrients, notably simple sugars, will be important positive factors."

The studies that have been conducted suggest that the proportion of fibre (cell wall polysaccharides) present in foliage are an important determinant of selection in both colobines and ruminants (Field, 1976; Stanley Price, 1977; Hoppe, 1977; Oates *et al.*, 1980; Choo *et al.*, 1981; Waterman, 1984; Davies *et al.*, 1988). Both these taxa have evolved digestive specialisations for breaking down fibre. In ruminants, the stomach has evolved into a multi-chambered vessel in which cellulose is fermented by a cellulase-producing microflora (Waterman, 1984). In the colobines, the fore-gut has been modified in a similar way (Chivers and Hladik, 1980), and in both groups volatile fatty acids are produced by a process of fermentation (Bauchop, 1978; Waterman, 1984). The howler monkey (*Alouatta palliata*) is another specialised folivore, in this case showing

modifications to the mid-gut; leaf selection in howlers, as in colobines and ruminants, also appears to be negatively correlated with fibre content (Milton, 1979).

Comparatively little is known about the principles underlying food selection in monogastric primates, such as the baboon. There is evidence that, like species specialised for a fibrous diet, they also possess populations of gut microflora enabling the breakdown of cellulose (Clemens and Phillips, 1980). However, because gut passage rates are considerably retarded by the fermentation process, its efficiency as a method of nutrient capture in monogastric species may be limited (Waterman, 1984). Furthermore, it appears that tannins may play a more important role in deterring feeding in monogastric primates than in colobines (Wrangham and Waterman, 1981). Finally, the ability to detoxify poisons found in many plant materials is thought to be less well developed in monogastric primates than in the colobines (Hladik, 1977).

These considerations suggest that primates probably vary, in some respects, in the rules underlying their dietary preferences. Unfortunately, it is currently difficult to say anything definitive about monogastric primates, due to the paucity of studies on them. Wrangham and Waterman (1981) examined diet selection in vervet monkeys (*Cercopithecus aethiops*), but focussed on the negative implications of condensed tannins. Until recently, very little was known, though occasionally quite a lot was assumed, about food preferences in the genus *Papio*. Data on phytochemical composition of baboon foods is now becoming available (Lock,

1972; Hausfater and Bearce, 1976; Hamilton *et al.*, 1978; Altmann *et al.*, 1987), but the work by Whiten *et al.* (in press) is the first comprehensive study of the rules underlying selective foraging in baboons. Their findings will be discussed subsequently, alongside results obtained here.

(a) Differences between foods and non-foods

The most common approach used in studies of determinants of food selection is to examine differences between foods and non-foods in the levels of various chemical constituents; some of these may have positive effects, and others may have negative effects. I have a relatively limited sample of non-foods for this type of analysis, mainly consisting of *Acacia* products. Thus, like Wrangham and Waterman (1981), I concentrate on selection amongst different parts and species of *Acacia*.

Phytochemical profiles for *Acacia* foods and non-foods are presented in Table 5.13, in the form of five matched samples. Thus, the seed kernels of each species in which these were eaten are paired with means for the two parts of the same species that were rejected (seed skins and pods), whereas means for whole dehiscent pods in species eaten are paired with means for the same parts in species not utilised. In general, protein content is higher in eaten items, while levels of fibre, condensed tannins and total phenolics are lower. The differences are significant in the case of protein ($t=3.72$, $df=4$, $p=0.020$), and total phenolics ($t=-14.19$, $df=4$, $p<0.001$). The differences are near-significant for fibre ($t=-$

TABLE 5.13: PHYTOCHEMISTRY OF *ACACIA* FOODS AND NON-FOODS

	Protein		Fibre	
Species/part	Food	Non-food	Food	Non-food
A.seyal seeds/pods	49.2	18.6	4.2	30.3
A.nilotica seeds/pods	47.0	11.8	3.1	16.6
A.tortilis seed/pods	39.9	10.8	10.1	29.6
Whole dehiscent pods	24.3	17.5	24.4	29.1
Flowers	22.2	12.8	13.1	12.2

	Condensed tannins		Total phenolics	
Species/part	Food	Non-food	Food	Non-food
A.seyal seeds/pods	0.4	8.6	0.5	6.5
A.nilotica seeds/pods	0.7	15.4	0.6	7.5
A.tortilis seeds/pods	1.2	10.2	0.4	6.4
Whole dehiscent pods	8.9	?	3.2	8.1
Flowers	2.7	3.6	4.4	10.7

2.59, df=4, p=0.060) and condensed tannins (t=-2.72, df=3, p=0.072), and if one argues that, since there is a strong prediction of the difference being in a particular direction (lower levels in foods than non-foods) a one-tailed significance test should be used here, the differences are significant. Note also the reduced sample size necessary in comparing tannin levels, due to the absence of an estimate for non-food whole dehiscent pods. It is interesting nevertheless, that the negative effect of total phenolics emerges more clearly than that of condensed tannins (the former theoretically includes the latter, but the two assays are based on different standards, so results cannot be directly compared).

Only crude quantitative assessments of alkaloid content are available. Of the seven food items, no alkaloids were detected in three, low levels were found in three, and medium levels in one. Of the seven non-food items, no alkaloids were found in five, low levels were found in one, and medium levels in one. In two other food items analysed, high alkaloid levels were found (Table 5.3). There is no evidence here, therefore, that alkaloids had a deterrent effect in terms of what items were incorporated into the diet. It is important to point out, however, that the assay method used did not distinguish between different types of alkaloids. The latter are a diverse group of chemicals with varying structure and activity (Waterman, 1984). It is therefore possible that particular types deter feeding, while others do not. It is worth noting that amongst the sample of pods that were not eaten, a

positive result (medium levels) was obtained for the pods of *A.nilotica*; this item had a surprisingly low fibre content (11.5%, compared to 29.6% and 37.9% for the pods of *A.tortilis* and *A.seyal* respectively), so perhaps an alkaloid is used by the plant as an alternative deterrant to herbivores.

Non-food counterparts of two other foods were also collected and analysed (Table 5.14). Ripe fruits of *Solanum incanum*, which were not eaten, had very similar levels of protein and fibre to unripe fruits, which were eaten. Neither contained any condensed tannins, but ripe fruits had marginally higher levels of total phenolics. The alkaloid assay indicated higher levels in ripe fruits than in unripe fruits, the reverse of the usual pattern found in the genus *Solanum* (Waterman, 1984). Corms of the sedge *Cyperus blysmoides* were usually dehusked by the baboons; the limited analysis that was possible on the small sample (about one gram) of corms with husks demonstrates higher fibre and tannin content than in dehusked corms. This accords with the comparisons between corms and corm "sheaths" in Altmann *et al.* (1987).

These analyses strongly suggest a positive effect of protein and a negative effect of total phenolics in determining which items will be incorporated into the diet. Low fibre and condensed tannin content were also associated with selection, if somewhat more weakly. No clear effect of alkaloid content could be demonstrated. It has, however, been argued by Whiten *et al.* (in press) that a distinction should be made between the rules underlying dietary selection and the actual dietary composition which the animals get as a result. Whiten *et al.*

(*ibid*) used a multivariate technique, discriminant analysis, to determine the weightings of the releyant constituents differentiating foods and non-foods. Though desirable, such an approach is not applicable to my small sample size; the conclusions of Whiten *et al.*, however, do not depart substantially from those suggested by the results reported here (see section 5.3 for further discussion).

(b) Preferences amongst food items

In this section I consider the influence of phytochemical composition on the degree to which different food items were preferred. I begin by examining selectivity across a broad array of food types and then narrow the focus to selectivity within particular types. Since predictions are being made about the direction of influence of the various factors, one-tailed significance tests are used unless otherwise stated. The possible role of alkaloids in determining feeding preferences is considered separately, since results of assays are expressed only on an ordinal scale.

(i) Nutrients and digestion inhibitors

It has aleady been shown that seasonal changes in the abundance of particular food classes influenced the contribution they made to the baboons' diet. The appropriate measure for assessing dietary preferences is therefore likely to be one that expresses preferences in terms of departure from the level of utilisation expected on the basis of abundance. The simplest and most commonly used such measure

is the selection ratio - simply the proportion of the diet divided by the proportion of the biomass.

Table 5.14 shows that, across all the major food types for which adequate biomass estimates are available (i.e. excluding herb roots and bulbs, and animal matter), the expected positive correlation between dietary percentage (mean of monthly percentage contribution to dry weight intake) and mean biomass is obtained. In contrast, none of the correlations between dietary percentages and phytochemistry are significant. Thus, differences in availability explain much of the variance in utilisation. When selection ratios are considered, however, significant correlations with protein content (positive) and fibre content (negative) emerge. If protein content is divided by fibre content (after Mckey *et al.*, 1981), this protein-fibre ratio correlates markedly better with selection ratios than do either protein or fibre on their own.

These results provide support for the conclusions of the preceding section; as expected, protein is positively associated with selection, while fibre is a negative factor. In order to examine whether secondary compounds or water content correlate with residual variation in preferences, I have calculated partial correlations between these variables and selection ratios, controlling for the effect of protein-fibre ratios. This yields a non-significant result for tannins ($r=^{-}0.084$, df=15, p=0.375), for total phenolics ($r=^{-}0.155$, df=15, p=0.276), and for the residual portion

TABLE 5.14: CORRELATES OF SELECTION AMONGST MAJOR FOOD TYPES

	MEAN % INTAKE		SELECTION RATIO	
	r	p	r	p
MEAN BIOMASS	0.528	0.012*	-	-
PROTEIN	-0.167	0.254	0.483	0.021*
FIBRE	0.300	0.113	-0.436	0.035*
TANNINS	-0.184	0.232	-0.159	0.265
PHENOLICS	-0.123	0.313	-0.155	0.367
PROTEIN/FIBRE	-0.279	0.131	0.829	<0.001**
PROTEIN/(FIBRE+TANNINS)	-0.262	0.147	0.853	<0.001**
RESIDUAL	-0.006	0.490	0.174	0.244
WATER	0.274	0.135	0.058	0.410

** $p<0.01$ * $p<0.05$

($r=^{-}0.081$, df=15, p=0.379), but a significant positive correlation for water (r=0.479, df=15, p=0.026). Thus it appears that water content may be a secondary factor underlying foraging preferences.

Waterman (1984) has emphasised that selection rules may vary according to the category of food under consideration, and most previous investigations of primates have focussed on leaf selection. Nevertheless, Wrangham and Waterman (1981) demonstrated the ubiquity of tannin avoidance across a range of *Acacia* products eaten by vervet monkeys (*Cercopithecus aethiops*). Recently, Whiten *et al.* (in press) found in their study of mountain baboons (*Papio ursinus*) that protein and fibre were consistent discriminators of foods and non-foods within all categories examined (see below for discussion of their findings). The results reported here provide further evidence for the generality of food selection principles, notwithstanding the lack of effects of secondary compounds. It may nevertheless be the case that these principles are modified when it comes to choices between food items of the same general type, so it is worthwhile to examine trends within types.

Data are available for ten types of foliage, ten types of non-sugary fruit (the latter including seeds/pods of two *Acacia* species), and six types of flower. Three bulbs and two succulents constitute an additional, "other" category. Correlations between biomass and dietary percentage are positive in each case, though not significant for flowers

TABLE 5.15: CORRELATES OF SELECTION RATIOS WITHIN FOOD TYPES

A. FOLIAGE (n=10)	r	p
PROTEIN	0.597	0.034*
FIBRE	-0.486	0.077
TANNIN	0.173	0.316
PHENOLICS	0.514	0.064
PROTEIN/FIBRE	0.616	0.025*
PROTEIN/(FIBRE+TANNIN)	0.640	0.023*
RESIDUAL	-0.287	0.210
WATER	0.038	0.462
B. FRUIT (N=10)		
PROTEIN	0.070	0.424
FIBRE	-0.330	0.176
TANNINS	0.198	0.292
PHENOLICS	0.245	0.250
PROTEIN/FIBRE	0.408	0.121
PROTEIN/(FIBRE+TANNIN)	0.149	0.348
RESIDUAL	0.096	0.389
WATER	0.271	0.178
C. FLOWERS (n=6)		
PROTEIN	0.557	0.126
FIBRE	-0.197	0.354
TANNINS	-0.163	0.379
PHENOLICS	0.674	0.071
PROTEIN/FIBRE	0.244	0.321
PROTEIN/(FIBRE+TANNIN)	0.388	0.206
RESIDUAL	-0.143	0.393
WATER	-0.100	0.425
D. BULBS+SUCCULENTS (n=5)		
PROTEIN	0.397	0.254
FIBRE	-0.194	0.377
TANNINS	-0.448	0.224
PHENOLICS	-0.172	0.391
PROTEIN/FIBRE	0.757	0.069
PROTEIN/(FIBRE+TANNIN)	0.666	0.110
RESIDUAL	0.137	0.413
WATER	0.838	0.038*

* $p<0.05$

(leaves, r=0.661, df=8, p=0.036; fruits, r=0.920, df=8, p<0.001; flowers, r=0.112, df=4, p=0. ; bulbs+succulents, r=0.867, df=3, p=0.028). Correlations between phytochemistry and selection ratios are presented in Table 5.15. In the foliage sample, selection ratios are positively correlated with protein content, and negatively, though not significantly with fibre content. As in the preceding analysis, the strongest correlation is with protein-fibre and protein-fibre+tannin ratios. No further relationships emerge when the effect of protein-fibre ratio is partialled out (tannins, r=⁻0.275; phenolics, r=0.187; residual, r=⁻0.065; water, r=0.161; p>0.05 in each case).

The influences of protein and fibre on selection within the other three food types is less clear; all the correlations are in the predicted direction (positive for protein, negative for fibre, and positive for protein-fibre ratios), but none are significant. For bulbs and succulents, the correlation with protein-fibre ratio is particularly close to significance (p=0.067). The residual proportion of dry weight was not significantly correlated with selection ratios in any of the food types.

Water content was positively correlated with selection ratios in the sample of bulbs and succulents. Partial correlations were therefore computed, holding constant the effect of water, to see if relationships then emerged with any of the other components; they did not (protein, r=0.611, p=0.194; fibre, r=⁻0.438, p=0.281; tannins, r=0.509, p=0.245; phenolics,

r=0.434, p=0.283; protein/fibre, r=0.709, p=0.145; protein/(fibre+tannin), r=0.492, p=0.254; residual, r=-0.476, p=0.262; df=2 in each case).

(ii) Alkaloids

Only seven foods were found to contain alkaloids, and, of these, adequate biomass data are available for only five. Table 5.16 shows that selection ratios for these five were generally lower than for foods yielding a negative result on the assay. The mean selection ratio for the three low-alkaloid foods was, in turn, considerably greater than for the higher-alkaloid items. Interestingly, the two foods with high and medium levels of alkaloid (young leaves of *Acacia brevispica* and flowers of *A.mellifera* respectively) also contained substantially more protein. One other food, the leaves of *Ammocharis tinneana* (for which biomass data are not adequate to compute selection ratios), also had high levels of alkaloids, and was also high in protein (31%). Thus, although caution must be exercised in the absence of larger sample sizes and the lack of information on the nature of the particular alkaloids involved, preliminary indications are that these chemicals had some effect on the food preferences of the baboons. Furthermore, it appears that plants producing growth rich in protein, and therefore of potentially high value to herbivores, may protect themselves with alkaloids.

TABLE 5.16: SELECTION RATIOS AND PROTEIN CONTENT FOR FOODS WITH VARYING LEVELS OF ALKALOIDS

ALKALOID LEVEL	MEAN SELECTION RATIO	MEAN % PROTEIN	N
HIGH	0.910	42.8	1
MEDIUM	0.780	34.6	1
LOW	2.711	19.6	3
NONE	3.390	20.6	32

(c) Discussion of food preferences in relation to phytochemistry

The results presented in this section have shown that diet choice was related to phytochemistry once relative abundance had been taken into account. As in the study of mountain chacma baboons (*Papio ursinus*) by Whiten *et al.* (in press), the positive influence of protein was particularly consistent, being apparent both in the differentiation of foods and non-foods, and in the degree of preference shown between foods. Levels of digestion-inhibitors (fibre, condensed tannins and total phenolics) were lower in foods than in non-foods, but correlations with selection ratios were generally not significant (the exception being fibre in the analysis conducted across food types). Nevertheless, correlations with protein-fibre ratios were mostly higher than those for protein on its own. In these respects, the findings suggest that rules governing dietary preferences were similar to those elucidated in colobines.

Whiten *et al.* (in press) found that a combination of positive factors (protein content) and negative factors (fibre,

alkaloid and total phenolics content) discriminated most effectively between foods and non-foods. There was some variation between food types in the discriminating factors, however; lipids emerged as a positive factor for sedge bases, whereas phenolics and alkaloids were not a problem for the subterranean items. The negative effect of fibre was less consistent than the positive effect of protein. Within food types in the present study, significant correlations between selection ratios and phytochemistry were restricted largely to the foliage sample. In part this may be a function of small sample sizes, and perhaps also of error in estimating biomasses of some foods, but it is also plausible that relevant aspects of phytochemistry have not been measured; a more comprehensive analysis would incorporate estimates for lipids, starch and simple sugars.

The lack of correlation between selection ratios and levels of condensed tannins and total phenolics is somewhat puzzling given that foods had significantly less of both than non-foods; it is worth bearing in mind the warning of Whiten *et al.* (in press) that demonstrating such differences is not equivalent to demonstrating the basis of selection, because it may be other, covarying, factors which are important. In the present case, significant differences were also obtained for both protein and fibre, and it may have been these alone that were determining selection. Nevertheless, the difference was more marked for phenolics ($p<0.001$) than it was for protein, fibre, or for protein-fibre ratios ($0.05>p>0.01$ in each case). Furthermore, Whiten *et al.* (in press) found that total phenolics did significantly improve discriminant functions in

their analysis, so it would seem premature to conclude that these compounds exerted no influence in the present case. Note that the near-significant *positive* correlations between selection ratios and phenolics within the sample of foliage can be explained by the fact that protein content and phenolic content were positively correlated in this type ($r=0.636$, $df=9$, $p=0.021$). This suggests both that plants protected leaves and flowers according to their protein content (and hence attractiveness to herbivores), and that the baboons were little deterred, if at all, by these phytochemical defenses. The implication is that plant defenses in this ecosystem are principally adaptations to the feeding activities of organisms other than baboons. In this context, Janzen (1978) has suggested that, at least in some habitats, insects are probably the driving force behind the evolution of phytochemical defenses.

The results obtained here provide the first demonstration that water content can exert a positive influence on diet selection in primates. In part this may be because it has infrequently been looked at, and Waterman (1984) states that, because the water content of leaves and fruit flesh is usually over 80%, water is not expected to be much of a problem. This is likely to be true for arboreal species living in forests, especially since the thermoregulatory burden of exposure to direct insolation will be largely absent (see Chapter 3). Gaulin (1979) argues that, because water takes up space in the gut that might otherwise contain nutrient-bearing material, high water content may actually deter feeding. Baboons both occupy environments exposing them to high temperatures and

prolonged insolation, and eat foods low in water (sedge corms and dry seeds are good examples). Whiten *et al.* (in press) did not find that water discriminated foods from non-foods, but their study population was living at high altitude, where temperatures were quite low and rainfall abundant (Whiten *et al.*, 1987). Wrangham (1981), however, observed vervet monkeys (*Cercopithecus aethiops*) at Amboseli subject to water stress in the dry season, and Wrangham and Waterman (1981) argued that this was due to the combination of low water availability and the high water requirements exerted by a diet rich in condensed tannins. Since standing water was available to subjects in the present study, it may seem surprising that water content played a part in food preferences. Waterholes were, however, sparsely distributed within the home range (see Chapter 3), and periods of several days were sometimes spent without utilising them; an interesting follow-up analysis would be to compare the water content of diets on days away from waterholes with those on days when waterholes were used.

An important feature of the results obtained by Whiten *et al.* (in press) was the negative influence of alkaloids in distinguishing foods from non-foods. Although the data were limited, results presented here also suggest avoidance of alkaloids. These findings tend to support the idea that, while the alimentary specialisations of colobines may facilitate detoxification of harmful substances, monogastric primates will be less capable of dealing with them (Hladik, 1977; Waterman, 1984). Nevertheless, some foods containing high levels of alkaloids were consumed (see Table 5.3). As noted above, prominent amongst these were the unripe fruits of

Solanum incanum. Alkaloids are usually withdrawn from fruit as it ripens (Mckey, 1974; Waterman, 1984), yet baboons often harvest immature fruits, bitter to human taste and avoided by other animals (Hamilton *et al.*, 1878). Ripe fruit of *S.incanum* has been fed to goats, sheep and rabbits without ill effect, but, in the rabbit, unripe fruit was found to cause acute catarrhal gastritis, haemorrages, emphysima of the lungs and dilation of coronary ventricles (Watt and Breyer-Brandwijk, 1962). The juice of the fruit is used in some areas as an arrow poison, but also as a remedy for pleurisy, pneumonia, toothache, ringworm, abdominal pains, and venereal diseases (Watt *et al.*). Perhaps it is the latter human applications that provide a clue for understanding the utilisation of this item by the baboons.

The view that some plant feeding in primates might be medicinal in function has been expressed by Janzen (1978), who notes, for example, that pomegranate (*Punicum granatum*) roots contain an alkaloid that is highly toxic to tapeworms, and that colobines in Kibale forest, which eat a leaf diet relatively high in secondary compounds, have lower levels of infestation than do sympatric monkeys which are more omnivorous. Wrangham and Nishida (1983) report possible medicinal usage of *Aspilia* leaves in chimpanzees (*Pan troglodytes*), and Phillips-Conroy (1986) argues that leaves and berries of *Balanites aegyptica* may have been eaten by baboons (*Papio hamadryas*) as a prophylactic agent against schistosomiasis. Huffman and Seifu (1989) have recently reported a case-study of an ill female chimpanzee apparently treating herself by chewing the pith of *Vernonia amygdalina*

and swallowing the astringent, bitter-tasting juice, which is also used by humans to treat intestinal cholic.

Solanum incanum was a very common plant at the study site, but its fruits were not particularly highly selected (selection ratio=0.85, where 1=unity between relative intake and relative biomass). They contained little protein (12.5% of dry weight), a medium amount of fibre (25%) and lipids (5.0%), and presumably small quantities of simple sugars. I often observed foraging baboons to walk straight past groves of *S.incanum* bushes with abundant unripe fruits. When individuals did feed on them, they appeared to take relatively few of the fruits available in the immediate vicinity; the maximum number I recorded eaten in a single bout was 27, by an adult male. Of course these observations do not preclude the possibility that the fruits were eaten for some nutritional benefits, and that individuals were simply constrained from eating too many by their toxicity. I would tentatively suggest, however, that this feeding pattern, coupled with what is known about their toxic properties and use by humans (Watt and Breyer-Brandwijk, 1962), may indicate a medicinal function. The most likely target would be gut parasites, such as nematodes and cestodes, with which baboons are invariably infested (Hausfater and Watson, 1976; Appleton *et al.*, 1986). The idea is speculative on the basis of the current evidence, and confirmation would require experiments demonstrating that the fruits, or extracts thereof, did indeed suppress or kill gut parasites. Perhaps the best evidence would be that baboons select fruits in response to experimental infection,

but data from the field on seasonal variation in diet and in parasite load would also be useful.

CHAPTER 6: NUTRIENT INTAKES

1. INTRODUCTION

Little is known about the nutritional requirements of free-ranging primates. This is certainly due in part to the methodological difficulties involved in measuring food intake. Close observation of feeding on identified foods, with some way of estimating quantities ingested, is necessary, and this may be impossible for most arboreal and cryptic species. Nevertheless, Hladik (1977) has emphasized the importance of measuring food intake, arguing that "time spent feeding cannot be accepted as an estimate of food intake, since feeding rate may differ considerably...". He has estimated daily intakes over 1-2 day periods for free-ranging howler monkeys *Alouatta palliata* (Hladik and Hladik, 1969) and langurs (*Presbytis senex* and *P.entellus*; Hladik, 1977). Gaulin and Gaulin (1982) also noted the difficulties of measuring food intake, but were able, in their lengthier study, to produce estimates for howler monkeys (*A. seniculus*) which were in close accord with the results obtained by Hladik and Hladik (1969). Whitten (1982), however, was able to measure food intake of gibbons (*Hylobates klossii*) only in one animal, under exceptional conditions, on a single day. Chivers (1974) was able to estimate intake rates of some, but not all foods in siamangs (*Symphalangus syndactylus*), due to poor visibility.

The difficulties are ameliorated in species which are largely terrestrial. Thus Watts (1988) measured daily dry weight intake in highly habituated mountain gorillas (*Gorilla gorilla beringei*). The visibility afforded in studies of largely

terrestrial, open-country cercopithecines, makes them ideal subjects for such work. Iwamoto (1979) estimated dry weight and energy intake in four adult gelada (*Theropithecus gelada*), while Stacey (1986) compared the energy balances of three different-sized groups of yellow baboons (*Papio cynocephalus*).

These successful studies suggest that estimation of food intakes in free-ranging primates is viable, and several issues remain to be addressed. In this chapter, I construct nutritional profiles by combining continuous feeding records with the data on phytochemistry and dry weights per bite (see Chapter 2 for methods). Daily food intakes were calculated assuming an active day length of 10.75 hours, which was the median observed duration (measured to the nearest quarter-hour) between descent from and ascent to the sleeping site (since the study site is close to the Equator, variation in daylength is minimal; range of monthly medians of active day = 0.5 hours; monthly variation in duration of active day was not significant; $F=0.827$, $df=9,52$, $p>0.05$). I also examine ingestion rates (intake of nutrients and secondary compounds per minute of feeding time). This information is then used to evaluate seasonal and sex differences in nutrition, nutritional costs associated with reproduction, and the influence of feeding competition (as reflected by dominance rank) amongst adult females. Average daily food intakes are also compared with predictions derived from allometric equations, and with measurements made in other studies of free-ranging primates.

2. EFFECTS OF MONTH, SEX, AND REPRODUCTIVE STATE ON FOOD INTAKE

Since the number of females in each reproductive state varied markedly between months (see Chapter 4), variation in feeding rates due to seasonal trends on the one hand, and to reproduction on the other, are likely to be confounded. One method of controlling these effects would be to calculate the mean of the monthly means for each reproductive state, and to then use reproductive state as the replicator variable for one-way ANOVAs investigating the effect of month, and, conversely, month as the replicator variable in a separate set of ANOVAs investigating the effect of reproductive state. This procedure has the disadvantages of being cumbersome, and of sacrificing information by pooling data for the calculation of means. A more economical (and more powerful) way of analysing the data is to enter the monthly values for each individual, assigned to cells according to reproductive state, into two-way ANOVAs, thereby analysing the effects of month and reproduction simultaneously.

Differences between females and males are also examined in this analysis; thus, for the purpose of the ANOVAs, "male" constitutes a reproductive state. Two additional dependent variables are also analysed; the ratio of protein to fibre ingested, and the percentage of time spent feeding. Results are presented in Table 6.1.

Each of the ANOVAs yielded significant overall F-values. Monthly variation was significant for ingestion rates of all food components (total dry weight, protein, fibre, tannins,

TABLE 6.1: RESULTS OF TWO-WAY ANOVAs TO INVESTIGATE THE EFFECTS OF MONTH AND REPRODUCTIVE STATE ON NUTRIENT INTAKE RATES, DIET QUALITY (PROTEIN/FIBRE), AND PERCENTAGE OF TIME SPENT FEEDING.

a)Ingestion rate (grams dry weight per minute feeding time^{-1}).

	Main effects: F value	Month F value	Repro state F value	Interaction F value
Total	6.62***	9.02***	0.94	1.97*
Protein	11.53***	16.00***	1.84	1.53
Fibre	3.482***	4.79***	0.46	2.09**
Tannins	26.44***	32.47***	1.56	1.08
Residual	7.68***	10.58***	0.98	1.93*

b)Daily intake (grams dry weight per 24 hours^{-1}).

	Main effects: F value	Month F value	Repro state F value	Interaction F value
Total	1.98*	1.86	2.45*	0.75
Protein	3.99***	5.01***	2.48*	0.66
Fibre	2.68**	3.11**	1.69	0.85
Tannins	17.21***	22.09***	3.25*	0.95
Residual	2.15*	2.09*	2.97*	0.95

c)Proportional composition and protein/fibre ratio of food ingested

	Main effects: F value	Month F value	Repro state F value	Interaction F value
% protein	11.86***	16.59***	1.71	0.83
% fibre	31.60***	44.93***	1.75	1.62
% tannins	11.38***	14.74***	1.63	1.03
% residual	15.91***	22.42***	0.93	1.26
P/F ratio	11.48***	16.15***	1.71	1.38

d)Percentage of time spent feeding

% Time	3.55***	2.33*	5.67***	0.91

*** $p<0.001$ ** $p<0.01$ * $p<0.05$

Notes: All rates and ratios log-transformed, percentages arcsine-transformed. Sexual states = cycling, pregnant, lactating, male. Months = May - December. Degrees of freedom = 10,3,7 (main effects), 21 (interactions).

and the residual portion), and also for daily intakes of each, excepting total dry weight. There was also significant monthly variation in diet quality (protein ingested/fibre ingested) and in the percentage of time spent feeding.

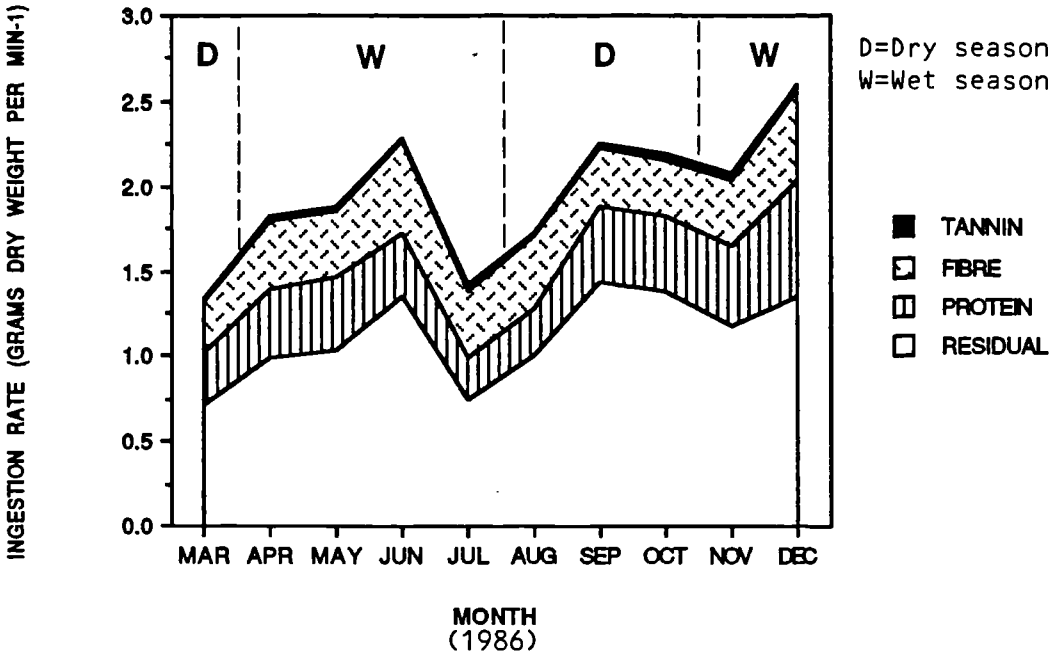
Ingestion rates did not vary significantly between reproductive states, for any of the food components. Daily intake of total dry weight, protein, tannin, and the residual portion, however, did show significant variation. Diet quality did not vary significantly between reproductive states, but the percentage of time spent feeding did.

These results, along with further analyses, will now be discussed in separate sections on seasonal variation, sex differences, and the influence of reproductive state.

3. SEASONAL VARIATION

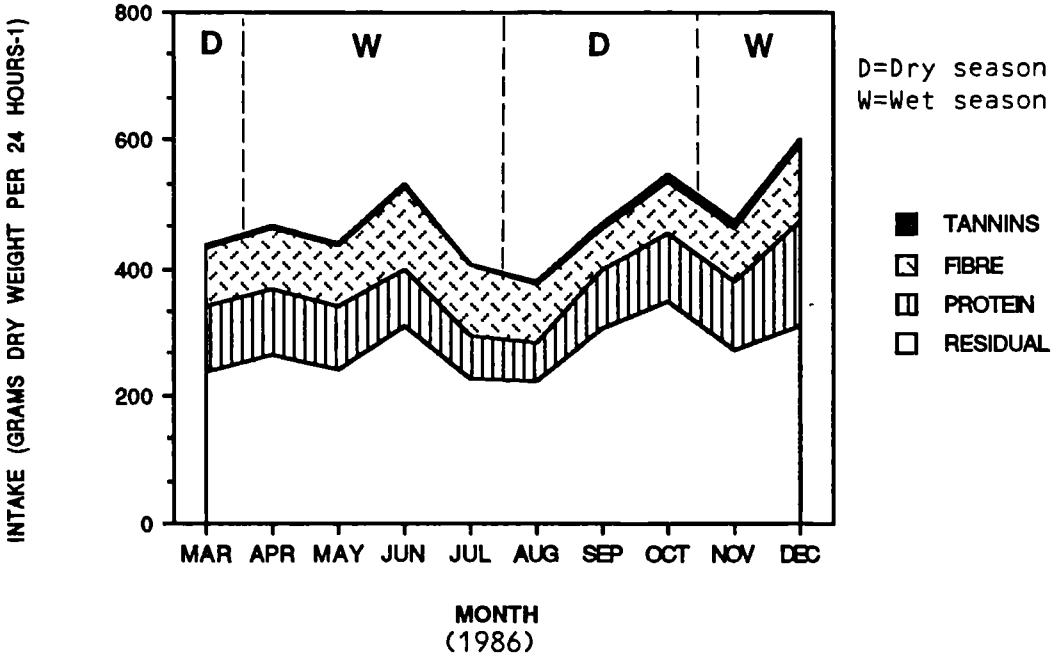
Figure 6.1 presents monthly variation in ingestion rates per minute of feeding time for protein, fibre, condensed tannins, and the residual portion. The top line on the graph therefore represents variation in total dry weight ingestion rates. The data points were calculated by averaging the monthly means for males and lactating, pregnant and cycling females. Similar data are presented in Figure 6.2, only in this case, values represent daily intake rates. In Figure 6.3, the data are re-expressed as percentage of dry weight intake made up by each component, and in Figure 6.4, protein/fibre ingestion ratios are presented.

FIGURE 6.1: MONTHLY VARIATION IN FOOD INGESTION RATES



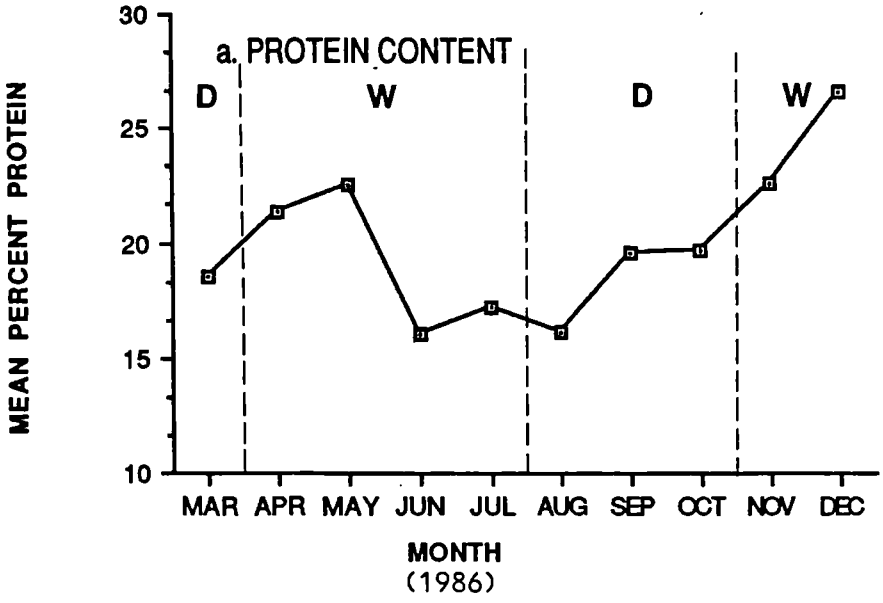
Ingestion rate is grams dry weight per minute of feeding time.

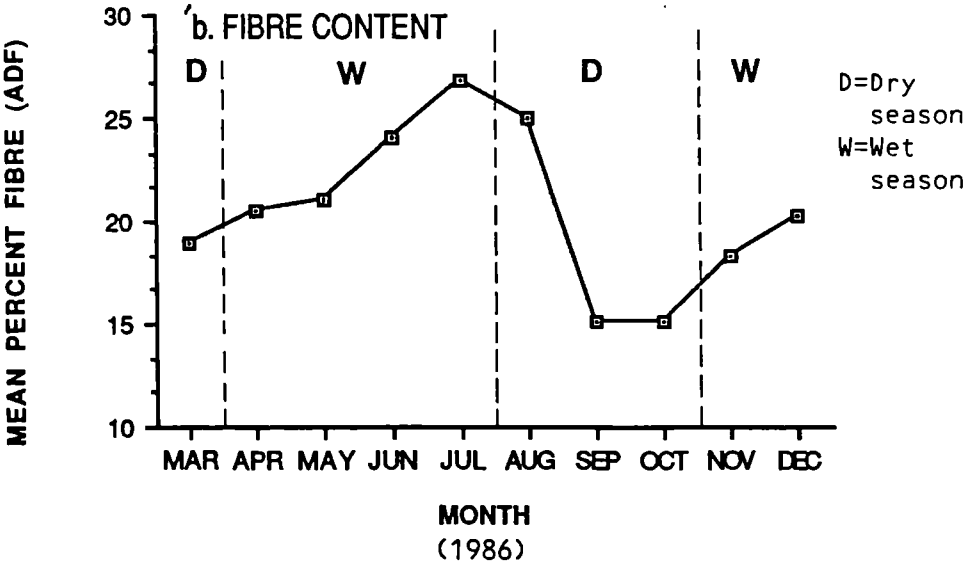
FIGURE 6.2: MONTHLY VARIATION IN DAILY FOOD INTAKES



Daily intake is grams dry weight per 24 hours.

FIGURE 6.3: MONTHLY VARIATION IN PROPORTIONAL COMPOSITION OF FOOD





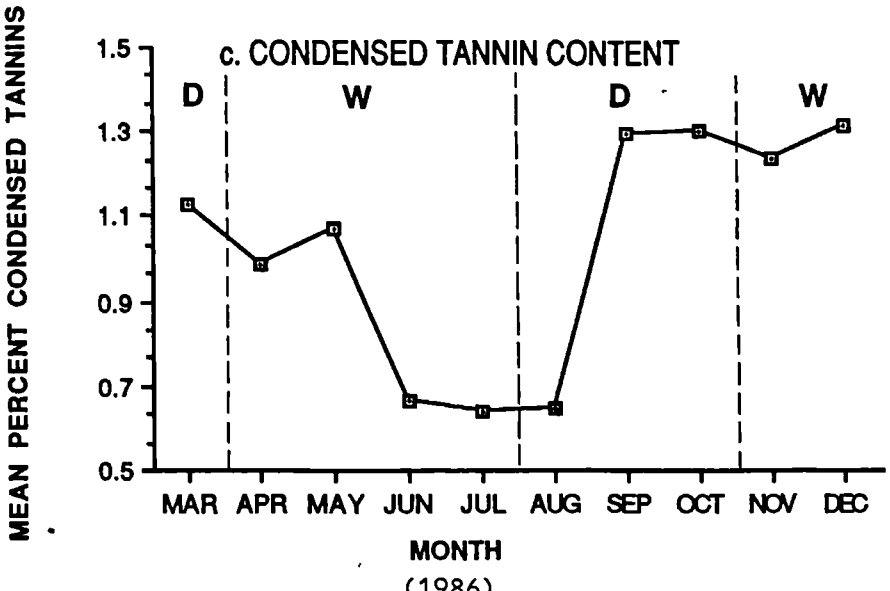
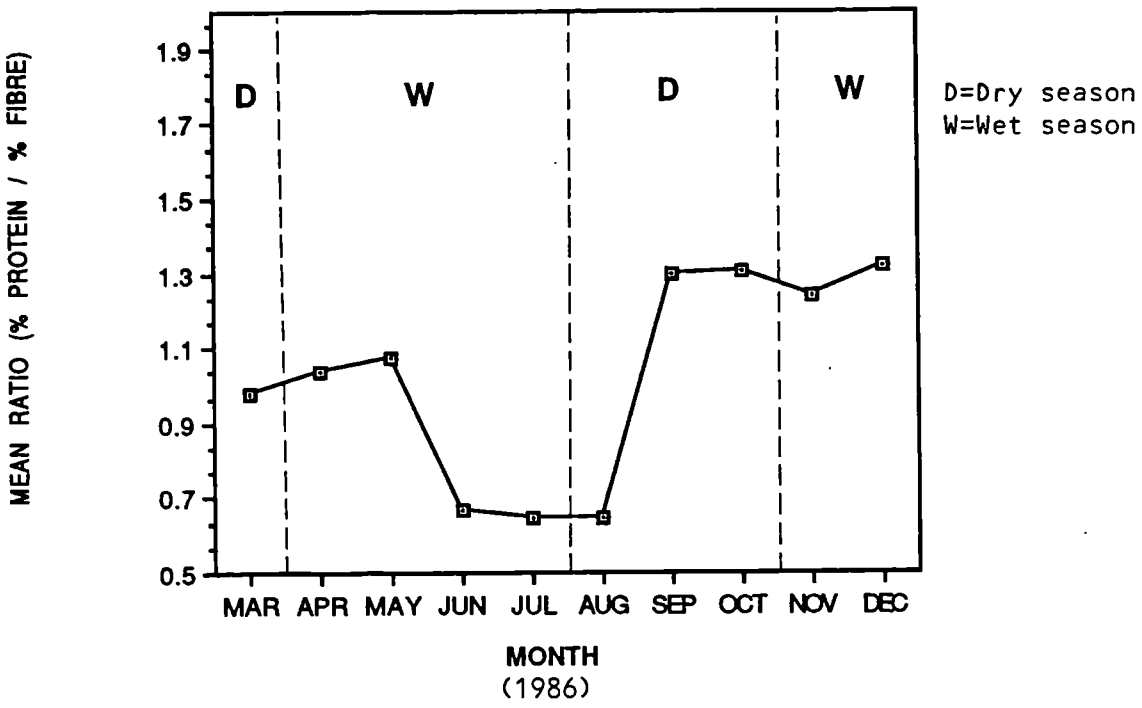


FIGURE 6.4: MONTHLY VARIATION IN PROTEIN-FIBRE RATIO OF FOOD



It has already been noted, from the results of the ANOVAs, that ingestion rates of all food components varied significantly on a monthly basis. Total daily dry weight intake, however, did not. It seems, therefore, that the baboons may have kept their daily intakes relatively constant, despite fluctuations in the rates at which nutrients could be harvested. If this were so, we would expect that they would have compensated for low harvesting rates by increasing the amount of time spent feeding; this idea is supported by a significant negative correlation between dry weight ingestion rate and percentage of time spent feeding ($r=-0.728$, $df=8$, $p=0.022$). Of course, dry weight intake only corresponds approximately to nutrient intake, because a proportion of it is indigestible, and the correlation is enhanced when we consider only the non-fibre, (hence digestible) portion of dry weight intake ($r=-0.834$, $p=0.005$). Nevertheless, presumably because the chemical composition of foods varied substantially, this was not enough to prevent there being significant variation in daily protein intake (Figure 6.3). One might expect to find increases in total daily intake to compensate for decreases in protein content, but, surprisingly, the reverse pattern is found (correlation between percentage protein content of diet and daily dry weight intake; $r=0.917$, $df=8$, $p<0.001$). Similarly, the ratio of protein to fibre ingested was positively correlated with daily intakes ($r=0.781$, $df=8$, $p=0.009$).

There is little evidence that these variations were related to overall seasonal productivity during the study period in any straightforward fashion; Table 6.2 shows that daily dry weight intake and dry weight ingestion rate were not

correlated with either baboon food biomass or rainfall. There were also no significant differences between dry months (March, August, September and October) and wet months (April, May, June and July) when the data were pooled accordingly (daily intake; t=0.72, df=8, p=0.492: ingestion rate; t=0.49, df=8, p=0.637). This lack of correlation must, however, be viewed in the context of the small sample size of eight months.

TABLE 6.2: CORRELATIONS BETWEEN FOOD INTAKE RATES AND ENVIRONMENTAL PARAMETERS

	Rainfall in month			
	Same	Previous	Previous two	Food biomass
a. Daily intake				
(i) Dry weight				
Pearson r	-0.043	-0.106	-0.200	0.313
df	8	8	8	6
p	0.908	0.772	0.580	0.450
(ii) Protein				
Pearson r	-0.053	-0.223	-0.561	0.124
df	8	8	8	6
p	0.884	0.528	0.088	0.728
b. Ingestion rate				
(i) Dry weight				
Pearson r	-0.096	-0.049	-0.199	0.250
df	8	8	8	6
p	0.792	0.892	0.580	0.550
(ii) Protein				
Pearson r	-0.129	-0.338	-0.259	0.071
df	8	8	8	6
p	0.722	0.350	0.554	0.840

Notes:
Daily intake in grams dry weight per 24 hours^{-1}, ingestion rate in grams dry weight per minute^{-1}, (log-transforms).

Were variations in the chemical composition of the diet related to extrinsic seasonal parameters? Table 6.3 displays

correlations with the proportion of the diet composed of protein, fibre, tannins, and the residual portion, and with the ratio of protein to fibre ingested. Three are significant, and although this is not particularly impressive given that we would expect $0.05(20) = 1$ "significant" result by chance, they are what we might expect given the phytochemical data in combination with the relationships between diet and rainfall reported in Chapter 5; percentage protein is positively correlated with rainfall for the previous month, reflecting high foliage consumption, while percentage fibre is positively correlated, and protein-fibre ratio negatively correlated, with rainfall for the previous two months, reflecting high consumption of herb fruits and grass inflorescences.

Differences in dietary composition between wet and dry months were non-significant for protein content ($t=1.40$, $df=8$, $p=0.199$), fibre content ($t=0.97$, $df=8$, $p=0.361$), and tannin content ($t=0.12$, $df=8$, $p=0.905$), but the residual portion was significantly greater in the dry season than in the wet season (dry season mean = 60.42%, wet season mean = 55.5%, $t=2.47$, $df=8$, $p=0.039$). The difference in protein-fibre ratios was not significant ($t=0.11$, $df=8$, $p=0.914$).

If energy expenditure on activities were determining daily food requirements, we might expect dry weight intake to be correlated with day range length and with components of the activity budget. The correlation with day range length is positive, but not significant ($r=0.352$, $df=8$, one-tailed $p=0.159$), and the same goes for the correlation with

percentage of time spent moving (r=0.252, df=8, one-tailed p=0.271). The same is found when considering intake of only the non-fibre (hence relatively digestible) portion of food (day range length; r=0.368, df=8, one-tailed p=0.142: time spent moving; r=0.418, df=8, one-tailed p=0.119).

TABLE 6.3: CORRELATIONS BETWEEN PROPORTIONAL COMPOSITION OF FOODS AND ENVIRONMENTAL PARAMETERS

	Rainfall in month			
	Same	Previous	Previous two	Food biomass
Protein				
Pearson r	0.167	0.660*	0.364	0.185
df	8	8	8	6
p	0.644	0.044	0.301	0.660
Fibre				
Pearson r	0.232	0.559	0.645*	0.423
df	8	8	8	6
p	0.518	0.092	0.044	0.296
Tannins				
Pearson r	0.062	-0.423	-0.513	-0.313
df	8	8	8	6
p	0.864	0.224	0.130	0.450
Residual				
Pearson r	-0.371	-0.544	-0.342	-0.521
df	8	8	8	6
p	0.292	0.104	0.334	0.186
Protein/Fibre ratio				
Pearson r	-0.110	-0.381	-0.641*	-0.236
df	8	8	8	6
p	0.762	0.278	0.048	0.574

* $p<0.05$

In the absence of clear statistical associations with environmental seasonality, some indication of the determinants of daily intakes and ingestion rates may perhaps be gained by a qualitative examination of trends during the study period.

If we look at Figure 6.1, it is apparent that both ingestion rates and daily intakes fluctuated considerably within seasons as well as between them. Thus, ingestion rates started at the low-point for the study period, in the first dry season, rising to a peak in the middle of the first wet season. They then dropped to another low point, before rising again in the following dry season. After a slight drop at the start of the second wet season, they reached the peak for the study period towards the end of it.

Daily dry weight intakes show a similar pattern, (although damped down by compensating changes in time spent feeding), and the two measures are highly correlated ($r=0.880$, $df=8$, $p<0.001$). The correlation could arise either because the animals fed faster when, for some unknown reason, daily energy requirements were high, or, perhaps more likely, daily intakes were partially constrained by the rate at which animals could feed. This could happen, for instance, if the animals were unable to entirely compensate for low feeding rates due to hitting a ceiling on feeding time (other activities, such as moving and socialising, must, to a degree, be conserved - Dunbar, 1988; Dunbar and Dunbar, 1989). Ingestion rate itself is presumably a composite function of the local biomass of food within patches and the speed with which it is processed. As an example, in Chapter 3 it was suggested that *Acacia* flowers occur in dense patches. Furthermore, *Acacia* flowers appeared to be simple to process, requiring no special processing technique. It is not surprising, then, that ingestion rates were relatively high when the baboons fed on this item (mean=2.446 grams dry weight minute^{-1}, compared to

the mean for all foods of 2.026 grams dry weight minute^{-1}). This can also explain the high overall ingestion rates (and hence daily intakes) in September and October, when a large proportion of the diet was composed of this item. Note that, although within-patch density may have been high at this time, overall biomass within the home range was low. Conversely, the two other peaks in ingestion rate both occurred during periods of relatively intensive utilisation of foliage, in the two wet seasons, when overall biomass was high.

We must conclude that ingestion rates are not related in any simple way to gross environmental fluctuations, but depend on both the local biomasses of particular food types and the speed with which they can be processed. To the extent that changes in time spent feeding only incompletely compensated for this variation, daily intakes are influenced by the same parameters. It is important to re-emphasize, however, that the seasonal variance sampled in the present study was limited, a point which is pursued in the discussion.

In Chapter 5 it was argued that foliage does not represent a low-quality, or high-fibre diet, in comparison with fruits. This is supported by the finding that monthly variation in the protein proportion of dry weight ingested correlates positively with the proportion of the diet made up by foliage ($r=0.752$, $df=8$, $p=0.012$), and negatively with the proportion of the diet made up by fruits (excluding leguminous seeds; $r=-0.672$, $df=8$, $p=0.034$). Conversely, the fibre proportion of ingested dry weight is uncorrelated with the proportion of foliage in the diet ($r=0.143$, $df=8$, $p=0.662$), but positively

correlated with the proportion of fruit in the diet (r=0.783, df=8, p=0.008). Finally, levels of tannin ingestion were also uncorrelated with the proportion of foliage in the diet (r=-0.059, df=8, p=0.876), but negatively correlated with the proportion of fruit in the diet (r=-0.662, df=8, p=0.037).

4. SEX DIFFERENCES

Mean daily intake rates and intake rates per minute of feeding time for males and females are presented in Table 6.4. In order to test for overall sex differences in nutrient intake rates, I have calculated monthly means for males and females and performed paired t-tests, with month as the replicator variable. In terms of daily intake rates, there was no significant difference for total dry weight (t=1.69, df=7, p=0.135), fibre (t=1.19, df=7, p=0.272), tannins (t=0.26,df=7, p=0.801), or the residual portion (t=0.98, df=7, p=0.384). The difference in daily protein intake, which favoured males, verged on significance (t=2.25, df=7, p=0.059). Total dry weight intake by females was 90.0% that of males. The general lack of differences in daily intake is reflected in high mass-specific intakes by females: body weights of males and females are estimated at 23.95 kg and 13.38 kg respectively (means of values for *P.anubis* given by Dunbar, in press, Table I), which implies daily dry weight intakes for males and females of 21.3 grams per $kg.^{-1}$ and 34.4 grams per kg. respectively, and daily protein intakes of 4.6 grams per kg. and 7.2 grams per kg. respectively.

TABLE 6.4: MEAN INTAKE RATES PER DAY AND PER MINUTE OF FEEDING TIME IN ADULT MALES AND FEMALES

	INTAKE IN GRAMS OF DRY WEIGHT	PROTEIN	FIBRE	TANNINS
a. INTAKE PER 24 HOURS^{-1}				
MALES	511.3	110.2	100.9	6.2
S.D.	(99.8)	(38.1)	(25.8)	(3.9)
FEMALES	460.1	95.9	94.0	6.4
S.D.	(77.4)	(31.6)	(18.7)	(3.9)
b. INTAKE PER MIN^{-1} OF FEEDING TIME				
MALES	2.120	0.453	0.416	0.027
S.D.	(0.476)	(0.160)	(0.099)	(0.016)
FEMALES	2.027	0.425	0.414	0.028
S.D.	(0.415)	(0.150)	(0.080)	(0.016)

Notes: Means and standard deviations (in brackets) are based on eight monthly values in each case.

In terms of ingestion rates (intake per minute of feeding time), again, no significant differences were found for total dry weight ($t=1.10$, $df=7$, $p=0.308$), fibre ($t=0.09$, $df=7$, $p=0.928$), tannins ($t=1.02$, $df=7$, $p=0.340$), or the residual portion ($t=1.46$, $df=7$, $p=0.189$). The difference in protein intake, once again favouring males, was significant ($t=2.65$, $df=7$, $p=0.033$), suggesting that the food eaten by males was marginally higher in protein than that selected by females. Despite this, the difference in the ratio of protein to fibre consumed was not significant ($t=0.88$, $df=7$, $p=0.409$).

A potential problem with the analysis of sex differences in feeding rates is that bite-size may have been greater for the larger-bodied males, for foods such as leaves and grass blades, where each bite is comprised of a sheaf gathered into the hand in successive plucking motions. Bites of such foods were differentiated according to size category,

but this is perhaps a rather crude way of controlling for the presumed confounding effect of body size. It was therefore deemed desirable to repeat the above analyses, including only foods for which bite size was universal, such as individual fruits, pods, seeds, flowers, *Euphorbia* stems, bulbs, corms and roots.

Dry weight intake of foods with universal bite sizes comprised 58.9% of the total intake of all individuals. Total daily dry weight intake of these foods by females was 92.6% that by males, which is actually a slightly larger proportion than the one calculated for total intake. Not surprisingly, then, when paired t-tests are computed with month as the replicator variable, the difference in daily dry weight intake is still not significant ($t=1.20$, $df=6$, $p=0.272$). In terms of dry weight ingestion rates per minute of feeding time, there was once again no significant difference ($t=1.03$, $df=7$, $p=0.340$). Assuming that these results are representative of total intakes, it seems that the lack of sex differences is not an artefact of a failure to control for differences in bite size.

In order to examine whether sex differences were more marked in particular periods of the study, uncorrelated t-tests were performed for each month, using individuals' monthly feeding rate scores. In terms of daily intake rates, there were no significant differences for any of the four components (dry weight, protein, fibre and tannins) in any of the eight months.

In the two-way ANOVAs (Table 6.1), there were significant interactions between the effects of month and reproductive state for ingestion rates of total dry weight, of fibre, and of the residual portion. Breaking the results down by month, males had higher rates for all four components in six out of eight months, but the differences were significant only for protein in September ($t=2.52$, $df=22$, $p=0.019$), and for total dry weight ($t=2.17$, $df=23$, $p=0.045$) and protein ($t=2.38$, $df=23$, $p=0.048$) in November. Females, however, ingested fibre at a near-significantly faster rate than males in September ($t=2.05$, $df=18.73$, $p=0.054$, separate variance estimate due to heterogeneity of variances). Overall, there may thus have been a slight tendency for males to eat faster than females; the differences in protein and fibre consumption per minute of feeding time in September is reflected in the fact that males had superior protein-fibre ratios in that month ($t=2.48$, $df=22$, $p=0.021$). Out of the other seven months, males' protein-fibre ratios were greater in six, but non-significantly so.

A word of warning, concerning experimentwise error rates, is appropriate once again; in the above analyses broken down by month, 72 t-tests were computed, giving rise to a total of 3 results significant at the 0.05 level. This is similar to the $0.05(72) = 3.6$ expected by chance, so the idea that males in general tend to eat faster than females should be treated with great caution.

In conclusion, the evidence for overall sex differences in the rates of food processing, in terms of both total daily intakes

and feeding speed, is, at best, slight. Males appear to have consumed marginally more protein, but this is not attributable to higher total food intake. Instead, the fact that protein, but not fibre or tannins, was ingested at a slightly higher rate per minute of feeding time by males, indicates that the quality of their diet may have been somewhat greater than that of females. Differences in protein-fibre ratios, however, were marginal, and were significant in only one month out of eight.

Possible reasons for the rather surprising lack of sex differences in food consumption rates and diet quality are taken up fully in the discussion at the end of this chapter. Meanwhile, it can be noted that, while pregnancy and, particularly, lactation are expected to be energetically costly for females, no account has yet been taken of their effects on food intake. This comprises the subject of the following section.

5. THE INFLUENCE OF REPRODUCTIVE STATE

In this section I examine the relationship between nutrient requirements and reproductive activity. Firstly, did the nutritional profiles of individual females reflect their reproductive histories during the study period? The answer appears to be yes; there are significant positive correlations between the percentage of months spent lactating and mean dry weight intake ($p=0.492$, $df=16$, one-tailed $p=0.019$), protein intake (0.444, $df=16$, one-tailed $p=0.032$), tannin intake ($r=0.408$, $df=16$, one-tailed $p=0.047$), intake of the residual

portion of dry weight (r=0.521, df=16, one-tailed p=0.013), and percentage of time spent feeding (r=0.863, df=16, one-tailed p<0.001). The correlation with fibre intake was not significant (r=0.311, df=16, one-tailed p=0.105). Ingestion rates, however, were not correlated with the percentage of months lactating (dry weight; r=-0.228, df=16, p=0.362: protein; r=-0.259, df=16, p=0.298: fibre; r=-0.357, df=16, p=0.146: tannins; r=0.009, df=16, p=0.970: residual portion; r=-0.149, df=16, p=0.556). Similarly, correlations between mean proportional composition of food ingested and the percentage of months lactating were not significant, although that for the residual portion nears significance (protein; r=-0.169, df=16, p=0.502: fibre; r=-0.390, df=16, p=0.110: tannins; r=-0.066, df=16, p=0.796: residual portion; r=0.465, df=16, p=0.052).

In accordance with the results presented above, the two-way ANOVAs (Table 6.1) indicated significant differences among reproductive states in daily intakes. Thus the high mass-specific daily intakes of females might reflect elevated nutritional requirements only at certain stages of the reproductive cycle. Tukey post-hoc tests on the ANOVAS yielding significant F-ratios (Table 6.1) are given in Table 6.5.

Table 6.5 shows that lactating females and males both had significantly higher daily total dry weight and protein intakes than pregnant and cycling females. Lactating females and males were not, however, significantly different from one another in these respects. The differences between pregnant

and cycling females were not significant either. Lactating and pregnant females each had significantly higher daily

TABLE 6.5: RESULTS OF TUKEY TESTS FOR DIFFERENCES AMONG REPRODUCTIVE STATES IN DAILY INTAKES AND PERCENTAGE OF TIME SPENT FEEDING.

a. TOTAL DRY WEIGHT

	Males	P.females	C.females
L.females	0.091	3.630*	3.780*
Males		3.701*	3.811*
P.females			0.151

b. PROTEIN

	L.females	P.females	C.females
Males	0.535	3.722*	3.986*
L.females		3.693*	3.718*
P.females			0.993

c. TANNINS

	P.females	Males	C.females
L.females	1.499	2.665	5.662***
P.females		1.166	4.163*
Males			2.988

d. RESIDUAL

	Males	P.females	C.females
L.females			
Males			
P.females			

e. % TIME FEEDING

	L.females	Males	P.females	C.females
L.females		2.272	4.673**	5.959***
Males			2.401	3.687*
P.females				1.286

Notes:
* p<0.05 ** p<0.01 *** p<0.001
L=Lactating; P=Pregnant; C=Cycling. Values in table are values of Tukey's Q statistic. Only variables for which the ANOVAs showed significant effects of reproductive state are included. Order of entries indicates descending rank order of means. For example, in (a), lactating females had highest intakes, followed by males, pregnant females and cycling females.

intakes of condensed tannins than did cycling females. Finally, lactating females spent the highest percentage of time feeding (mean=43.0%), the differences with pregnant females (mean=35.4%) and cycling females (mean=34.5%), but not with males (mean=38.5%), being significant. Daily food intakes for females in each reproductive state are presented in Table 6.6.

TABLE 6.6: MEAN DAILY INTAKE RATES FOR FEMALES IN EACH REPRODUCTIVE STATE (GRAMS DRY WEIGHT PER 24 HRS^{-1})

	INTAKE IN GRAMS OF			
	DRY WEIGHT	PROTEIN	FIBRE	TANNINS
LACTATING	518.8	105.4	101.4	7.7
S.D.	(129.0)	(30.8)	(15.5)	(4.3)
PREGNANT	454.4	96.0	96.1	5.9
S.D	(196.1)	(38.9)	(56.8)	(3.8)
CYCLING	442.5	88.4	86.1	5.3
S.D	(102.3)	(40.6)	(23.4)	(4.1)

Notes: Means and standard deviations (in brackets) are based on eight monthly means for each reproductive state.

These results confirm that there are tangible nutritional costs associated with lactation, if not with pregnancy. They also show that sex differences in daily nutrient intakes do exist, but are contingent on the reproductive states of females. Intriguingly, nutrient intakes of males and lactating females were remarkably similar, despite the great disparity in body size; the implications of this finding are taken up in the discussion.

Some toxins have been shown to have detrimental effects on foetuses when ingested by pregnant females, and even to appear in the milk of lactating animals (Watt and Breyer-Brandwijk,

1962; Janzen, 1978). Measures of the absolute quantity of alkaloids in plant foods are not available, but an indication of amounts ingested can be obtained by examining the percentages of food eaten which yielded a positive alkaloid test (see Table 5.3). Data are presented in Table 6.7.

TABLE 6.7: ALKALOID INTAKE ACCORDING TO REPRODUCTIVE STATE

	MEAN PERCENTAGE OF FOOD WITH: HIGH ALKALOID LEVELS	ANY ALKALOIDS
CYCLING	1.31	25.13
S.D.	(1.89)	(22.85)
PREGNANT	0.41	19.28
S.D.	(1.04)	(20.34)
LACTATING	0.92	26.74
S.D.	(1.50)	(23.76)
MALES	2.22	33.19
S.D.	(4.13)	(24.68)

Notes:
Values are means and standard deviations of monthly means (n=8) for each reproductive state.

It can be seen that, whether one considers all alkaloid-containing foods or only foods containing high levels, pregnant animals consumed the smallest proportional amounts, and males the largest proportional amounts. Differences between lactating and cycling females were not clear-cut, the former consuming slightly less high-alkaloid food, but more alkaloid-bearing food generally. The differences among reproductive states (including males) in the percentage of intake made up by all alkaloid-bearing foods are significant (repeated-measures ANOVAs with month as replicator variable: high-alkaloid foods; $F=3.143$, $df=3,21$, $p=0.049$).

Tukey post-hoc tests reveal that percentage intake was significantly greater in males than in pregnant females ($Q=4.420$, $p=0.024$), but that none of the other differences were significant (males vs. lactating females; $Q=2.195$, $p=0.426$: males vs. cycling females; $Q=2.210$, $p=0.464$: cycling females vs. lactating females; $Q=0.511$, $p=0.900$). Due to the large number of cells containing zeros, a similar analysis of intake of high-alkaloid foods was not viable.

6. NUTRIENT INTAKES IN COMPARATIVE PERSPECTIVE

This section is concerned with two questions. Firstly, how do the estimates of daily nutrient intake compare with predictions derived from allometric equations? Secondly, do the limited data already available for free-ranging primates show a regular relationship with body size, and therefore imply that methodologies are sufficiently accurate and robust to validate future comparative studies?

a. Comparison of observed and predicted nutrient intakes

Basal metabolic rates of mammals are described by the allometric equation:

$$BMR = 317\ W^{0.75} \qquad (1)$$

(Kleiber, 1961; Linstedt and Boyce, 1985), where BMR is in $kJ \cdot day^{-1}$, and W is body weight in kilograms. Using mean body weights of olive baboons calculated from Dunbar (in press,

Table I) the BMRs of males and females can thus be estimated as:

$$\text{Male} \quad BMR = 317\ 23.95^{0.75} = \underline{3432\ kJ \cdot day^{-1}} \qquad (2)$$
$$\text{Female} \quad BMR = 317\ 13.38^{0.75} = \underline{2218\ kJ \cdot day^{-1}} \qquad (3)$$

Unfortunately, energy values of foods eaten have not been determined in the present study. Stacey (1986), however, estimated the physiological fuel value (PFV) of foods in his study of yellow baboons (*P.cynocephalus*); since there is considerable overlap in the diets of these two populations (see Chapter 5), it seems reasonable to assume similar energy values. The mean PFV in Stacey's study was 13.98 kJ per gram dry weight^{-1} (calculated from his Table 3). Interpolating the intake values in Tables 6.2 and 6.4 yields daily energy intakes of 7144 kJ for males, and 6432 for females. These values imply total energy requirements greater than BMRs by factors of 2.08 and 2.90 respectively, consistent with the conclusion of Peters (1983) that daily energy expenditure in homeotherms are approximately " two to three times basal ". Breaking the female data down according to reproductive state (Table 6.4) yields daily energy intake values of 7242 kJ for lactating females (3.3 times basal), 6347 kJ for pregnant females (2.9 times basal), and 6179 kJ for cycling females (2.8 times basal).

Allometric equations describing energy intake are provided by Peters (1983; citing Farlow, 1976). For homeotherms, energy intake is predicted as:

$$EI = 10.7\ W^{0.703}\ J \cdot sec^{-1}, \text{ or } 924.4\ W^{0.703}\ kJ \cdot day^{-1}. \qquad (4)$$

Again interpolating the body weights in equation 1, predicted daily intakes are 8620 kJ for males and 5725 kJ for females. Observed values (above) were lower in males, but higher in females, and the mean of the predicted values is tolerably close to the mean of the observed values (7173 kJ and 6788 kJ respectively). While the mean intake of lactating females, at 7242 kJ, was considerably higher than predicted, that of cycling females, at 6179 kJ, was only about 1.1 times greater.

Voluntary nitrogen intake is described by the equation:

$$N_2 = 1.60\ W^{0.75}\ \text{grams}\cdot\text{day}^{-1} \qquad (5)$$

(Peters, 1983; citing Evans and Miller, 1968). Assuming a conversion factor of $N_2 * 6.25$ (Crampton and Harris, 1979), predicted protein intakes are:

$$\text{Male} \quad PI = 10.0\ 23.95^{0.75} = \underline{108.3\ \text{grams}\cdot\text{day}^{-1}} \qquad (6)$$
$$\text{Female} \quad PI = 10.0\ 13.38^{0.75} = \underline{69.9\ \text{grams}\cdot\text{day}^{-1}} \qquad (7)$$

The prediction for males is remarkably close to the observed value of 110.2 grams·day^{-1}, while the prediction for females is somewhat below the range of observed values for females in different reproductive states (88.4-105.4 grams·day^{-1}).

In conclusion, two main observations can be made. Firstly, estimated energy and protein intakes were much as predicted from comparative data, with energy intakes roughly two to three times the requirements dictated by basal metabolism; this encourages the idea that reasonably accurate estimations of these parameters can be obtained in studies of free-ranging

animals. Secondly, energy and protein intakes by females were higher than the predicted values, and markedly so in lactating females, emphasising once again the nutritional costs of reproduction.

(b) Allometry of dry weight intakes in free-ranging primates

Six published studies were located in which food intakes were measured. Body weights were extracted from Stacey (1986), Iwamoto (1979), Dunbar (in press), and from a data-base kindly made available to me by Professor R.D. Martin. This information, along with results from the current study, is presented in Table 6.8. Unfortunately, separate food intake estimates for males and females are provided in only one other study (Iwamoto, 1979, on *Theropithecus gelada*). In the study of mountain gorillas (*G. gorilla berengei*) by Watts (1988), only data for females were published. In all other cases, means of male and female body weights are used, and food intakes for *T.gelada* and *P.anubis* are also means of values for males and females.

TABLE 6.8: DAILY DRY WEIGHT INTAKES OF FREE-RANGING PRIMATES

SPECIES	BODY WEIGHT(kg)	INTAKE(g. 24 hours^{-1})
1.Alouatta seniculus	7.3	266
2.Papio anubis	18.7	492
3.Papio cynocephalus	14.8	408
4.Theropithecus gelada	18.5	898
5.Presbytis entellus	12.8	321
6.Presbytis senex	8.2	188
7.Gorilla g. berengei	93.0	2955

Sources: 1 - Gaulin and Gaulin (1982); 2 - present study; 3 - Stacey (1986); 4 - Iwamoto (1979); 5+6 - Hladik (1977); 7 - Watts (1988).

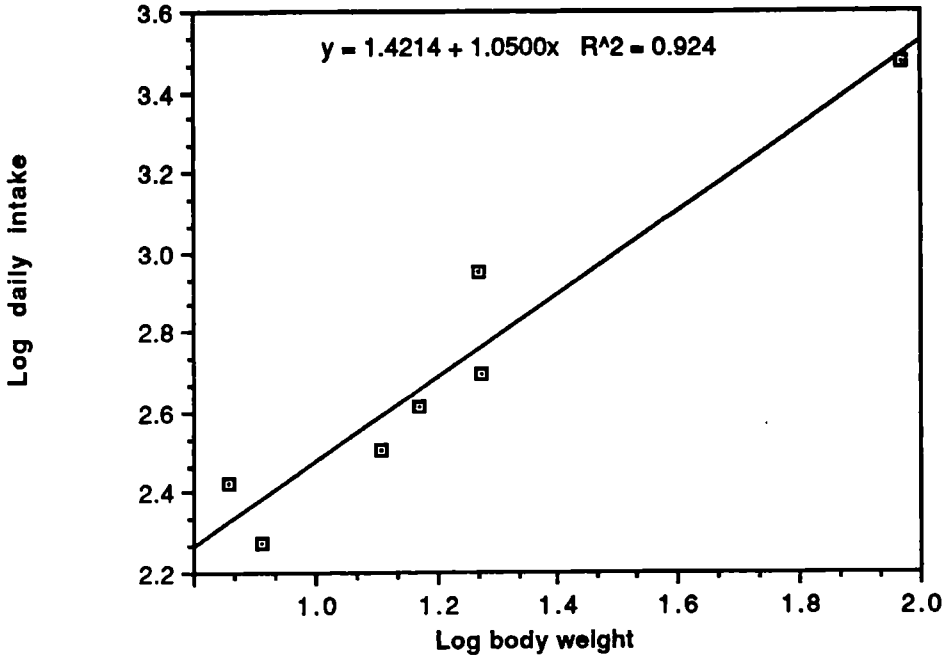
Figure 6.5 displays the least-squares regression of daily dry weight intake on body weight, after logarithmic transformation of both variables. The regression is highly significant, with over 90% of the variance in daily intake accounted for. The equation describing the relationship is:

$$\log \text{intake} = 1.05 \cdot \log \text{body weight} + 1.421 \qquad (8)$$

The relationship appears to be approximately linear; clearly, more data are required before any firm emphasis can be placed on the value of the scaling exponent (1.05 in equation 8), but it is interesting to note that Nagy's (1987) analysis of field metabolic rates, measured by the doubly-labelled water technique, indicated a scaling exponent for eutherian mammals significantly greater, at 0.813, than the 0.75 expected on the basis of scaling of basal metabolic rates (Kleiber, 1961; Peters, 1983). Nagy and Milton (1979) examined field metabolic rates of howler monkeys using the doubly-labelled water method, and also found a least-squares regression scaling exponent close to unity. The slope of the line in allometric analyses is known to be influenced by the method used, and the major axis and reduced major axis are considered preferable to model 1 regression (Harvey and Mace, 1982; Pagel and Harvey, 1988). Model 1 regression, however, tends to *underestimate* the slope relative to that obtained by the other methods (e.g. Martin and Harvey, 1985).

The most noticeable deviation from the regression line in Figure 6.5 is the point for *T. gelada*. While the mean body weight of the gelada is very similar to that of olive baboons

FIGURE 6.5: RELATIONSHIP BETWEEN DAILY FOOD INTAKE AND BODY WEIGHT IN PRIMATES



Daily intake in grams dry weight per 24 hours, Body weight in kilograms. Regression determined using "CRICKET" graphics package.

(18.7 versus 18.8 kilograms), estimated food intakes were 1.8 times greater. Perhaps the most plausible explanation for this is the metabolic cost of thermoregulation. Iwamoto's study group lived at high altitude (about 4000 metres above sea-level), and night-time temperatures dropped to 0°C in the dry season. Mean temperatures were only 6-9°C. Iwamoto and Dunbar (1983) found a positive correlation between altitude and time spent feeding among populations of gelada, and concluded that this reflected differences in the energetic costs of thermoregulation. Low diet quality may also be a contributory factor to large food intake in this species (Dunbar, 1988). Comparative data on dry weight intake from other primate populations living in extreme climatic conditions, as well as information on phytochemistry of gelada foods, are needed to evaluate these hypotheses. Interestingly, Whiten *et al.* (1987) report that chacma baboons (*Papio ursinus*) inhabiting a high-altitude sub-alpine habitat similar to the lower zones of the gelada's, were "at the high end of the foraging-time distribution" for baboons, although they attribute this to the heavy dependence on underground foods, which require extensive processing time.

In conclusion, it appears that the estimates of daily food intake, made by different researchers working independently, show a regular relationship with body size. This finding provides further encouragement for the view that accurate determinations of intake are possible, opening up the possibility of future comparative analyses of the effects of parameters such as diet and temperature.

7. THE INFLUENCE OF DOMINANCE RANK AMONGST FEMALES

This section addresses the question of whether the nutritional profiles of individual adult females were influenced by their status in the dominance hierarchy (see Chapter 4). The ways in which such influence might operate are then examined in Chapter 7.

Mean intake rates were computed for each of the 18 adult females, as the average of their monthly values for the period May-December. Using these means, with df=16, significant positive correlations are found between dominance rank and daily intakes of total dry weight (r_s=0.540, p=0.020), protein (r_s=0.527, p=0.024), fibre (r_s=0.552, p=0.018), and the residual portion (r_s=0.486, P=0.040), but not tannins (r_s=0.224, p=0.372).

Looking at the magnitude of these effects, the mean daily dry weight intake of the three top-ranking females was 559 grams, compared to a mean of 393 grams for the three bottom-ranking females. Low rank, by this criterion, was therefore associated with a 30% depression in food intake. This compares with differences between top- and bottom-ranking female vervets (*Cercopithecus aethiops*) and capuchins (*Cebus capuchinus*) of 16% and 30% respectively (Janson and van Schaik, 1988).

The mean percentage of time spent feeding was not correlated with dominance rank (r_s=0.065, p=0.399), suggesting that the

intake differentials resulted from differences in ingestion rates (per minute of feeding time). This is confirmed; dominance rank was positively correlated with ingestion rates, in the cases of total dry weight (r_s=0.754, p<0.001), protein (r_s=0.624, p=0.006), fibre (r_s=0.542, p=0.020), and the residual portion (r_s=0.756, P<0.001), but again not tannins (r_s=0.133, p=0.598).

Dominance rank was not correlated with the proportional chemical composition of food ingested (protein; r=$^-$0.304, p=0.220: fibre; r_s=0.205, p=0.414: tannins; r_s=$^-$0.195, p=0.438: residual portion; r_s=0.349, p=0.158). Nor was there a significant correlation between dominance rank and mean protein-fibre ratio (r_s=$^-$0.100, p=0.346).

As we have seen, daily intakes correlated significantly with the percentage of months spent lactating during the study period. There is, however, no association between rank and the percentage of months lacatating (r_s=0.095, p=0.708). Furthermore, if the influence of reproductive costs is controlled by correlating rank with the residuals from regressions of daily intakes on percentage of months spent lactating, there is no substantial departure from the findings reported above (dry weight; r_s=0.511, p=0.030: protein; r_s=0.488, p=0.046: fibre; r_s=0.548, p=0.018: residual portion; r_s=0.521, P=0.026). This is also true when the same type of analysis is performed for ingestion rates (dry weight; r_s=0.736, p<0.001: protein; r_s=0.695, p=0.002: fibre; r_s=0.620, p=0.006: residual portion; r_s=0.713, P<0.001).

In conclusion, this section provides clear evidence for a positive relationship between dominance rank and nutrient intake rates, mediated by ingestion rates rather than percentage of time spent feeding, but no evidence for rank-related differences in the quality of food ingested.

8. DISCUSSION

a) Seasonal variation and some comparative trends in nutrition

There was marked seasonal variation in ingestion rates, and reciprocal variation in the percentage of time spent feeding; thus daily intakes remained relatively constant. I have suggested that ingestion rate nevertheless partially constrains daily intake, because of limits on the extent to which feeding time can be increased to compensate; this requires verificaton. Neither ingestion rate nor daily intake bore any simple relation to extrinsic seasonality as measured (rainfall and food biomass). There was also substantial seasonal variation in the chemical composition of the diet, and this did show some relationship with the measured environmental variables.

There is only one other published study examining seasonal variation in nutrient intakes of free-ranging primates. This is the study by Hladik (1977), comparing the feeding strategies of two colobines, *Presbytis entellus* and *Presbytis senex*. As in the present study, there was substantial monthly variation in chemical composition of the diet, though *P.senex*

varied less than *P.entellus*. The protein proportion of the diet was fairly constant at around 11% in *P.senex*, and fluctuating between 10-16% in *P.entellus*. In contrast, 16% was the seasonal low-point for the baboons, rising as high as 27% at the end of the study period. This difference reflects the evolutionary divergence of colobines and cercopithecines, the former developing foregut specialisations for digesting relatively low-quality, high-fibre foods via fermentation, the latter retaining a simple foregut, and capable of only limited fermentation (Clemens and Phillips, 1980; Waterman, 1984).

Hladik (summarised in Richard, 1985, pp.155-159) has also published average chemical compositions of diets for several other haplorhine species. In the howler monkey (*Alouatta palliata*), protein made up 9.6% of the diet, and this species also has morphological specialisations for folivory (Milton, 1981). Spider monkey (*Ateles geoffroyi*) diet was also low in protein (7.4%), but high in readily digestible simple sugars (34%). Cebus monkeys (*Cebus capuchinus*) consumed more protein (14% - about the same as *P.entellus*), and also quite high levels of simple sugars (26%). None of these species had cellulose components anywhere near those in the diets of the two colobines. Unfortunately, the figures for cellulose in these studies are not directly comparable with the figures for fibre (ADF) in the present one, but it is evident that baboons pursue a "high-protein" strategy, with simple sugars almost certainly being a less important component than for the cebids, but with a fibre intake lower than the colobines.

Hladik (1977) noted that protein consumption was highest during the rainy season, when immature foliage comprised a large part of the diet, whereas simple sugar intake followed seasonal variation in availability of fruits and flowers. I found a similar correlation (between protein/fibre content of the diet and utilisation of foliage), and this was related to rainfall, through the effects of the latter on the production of new young foliage, much favoured by the baboons.

The lack of association found between environmental parameters and both ingestion rates and daily intakes in this study, should not be considered conclusive. The period during which feeding data were collected (March - December) was not one of very great seasonal fluctuations, since it excluded most of the first dry season, which was considerably more severe than the second one. Since ranging data were collected from January, it is not surprising that day range length displayed more environmentally-related variance, reflecting dry season shortages, (Chapter 3) than did feeding. Subsequently, collection of feeding, ranging and ecological data has continued into the medium-to-long term, so it should eventually be possible to perform more comprehensive analyses of the interrelationships between these variables over periods incorporating more seasonal variance.

b) Sex differences: the energetic impacts of reproduction, thermoregulation and activities, and the implications of diet quality.

Previous findings have suggested, though not conclusively demonstrated, that the food intakes of male and female primates of dimorphic species are unexpectedly similar. It

has often been found that females spend scarcely less time feeding than males, or even that they spend more time feeding (Clutton-Brock, 1977; Post *et al.*, 1980; Post, 1981; Harcourt and Stewart, 1984; Watts, 1988; Rhine, in prep.). A similar finding has been made by Clutton-Brock *et al.* (1982) in red deer (*Cervus elephus*). These observations, however, suffer from the problem that they take no account of feeding rates, and hence may not reflect nutrient ingestion. This would be the case, for example, if females for some reason fed less efficiently than males, as suggested by Clutton-Brock (1977).

The results presented here circumvent the problem, and demonstrate that the difference in nutrient intakes is far less than that expected on the basis of the scaling laws linking energy requirements to body size. Similar findings can be extrapolated from the data presented by Iwamoto (1979), who recorded daily dry weight intakes of 971.4 g. and 825.3 g. respectively for male and female gelada (*Theropithecus gelada*), suggesting that female intakes were about 85% those of males. Using Iwamoto's body weight estimates of 23 kg. and 14 kg., we can calculate that, according to Kleiber's law, female intakes "should" have been $(14/23)^{0.75} = 68.9\%$ of male intakes. Likewise, in Watts' study of gorillas (*Gorilla g. berengei*), females fed for only slightly less time than silverback males, and the latter did not have higher ingestion rates. Finally, van Schaik and van Noordwijk (1986) found that the rates of fruit ingestion by long-tailed macaques (*Macaca fascicularis*) differed little between adult males and females.

In the present study, female intakes were about 90% those of males. Possible reasons for this small difference are: physiological costs of reproduction; some other energetic cost disproportionately related to body size, such as thermoregulation; greater energy expenditure by females on activity; relatively low diet quality in females. These hypotheses will be dealt with individually below.

(i) Reproduction

The physiological costs of reproduction evidently did elevate the nutrient intakes of females. It has been suggested that, in mammals, basal energy requirements increase by factors of about 15-25% during pregnancy (Portman, 1970; Clapp et *al.*, 1971; Begley *et al.*, 1980; Bronson, 1985) and about 30-50% during lactation (Hytten and Thomson, 1961; Portman, 1970; Bronson, 1985) . In the present study, estimated daily energy intakes were on average 168 kJ and 1063 kJ lower in cycling females than in pregnant and lactating females respectively. Against the estimated basal metabolic rate of 2218 $kJ \cdot day^{-1}$, this represents increases of about 7.5% and 48%.

Data on the energetics of lactation in baboons are available for comparison from laboratory studies. In a review, Oftedal (1984) reports that at peak lactation daily milk energy output in *P.cycnocephalus* is 162 kJ $W^{0.75}$. For our typical 13.38 kg female olive baboon, this implies a daily energy output of 1133 kJ, equivalent to a 51% increment of basal metabolic rate. Roberts *et al.* (1985) determined energy intakes in captive *P.cynocephalus* and *P.anubis*. The average total energy intake by females during lactation was 17.6% higher

than during the non-reproductive weight-maintaining phase, being remarkably close to the difference of 17.2% between lactating and cycling females in the present study. Total energy intakes were, however, slightly lower in the study by Roberts *et al.*, despite the fact that their animals were heavier (about 20 kg) than most wild females (this is not too surprising given the lower energy requirements for activity and thermoregulation in the captive setting).

The increase in food intake by lactating females was clearly within the range expected, while that for pregnant females was much less than expected; indeed, the differences between pregnant and cycling females were not significant. Altmann (1980) and Dunbar (1988) have explored the time-budgetting costs of lactation in wild baboons (*P.cynocephalus*) and gelada (*Theropithecus gelada*). Their data suggest that, at peak lactation, females' feeding budgets are elevated by between 40% (Altmann's data) and 79% (Dunbar's data; estimated from his Figure 2), to values well above the time spent feeding by adult males. These figures compare with an *overall* difference of 23% more time spent feeding by lactating females than by cycling females in the present study.

Here, then, we have at least a partial explanation for the small difference in average food intakes of males and females; the requirements of the latter are, during the phase of peak energetic costs, raised to a level which is at least equal to, and probably greater, than those of males. It is important to bear in mind that I have not estimated food intake at peak lactation, though this will inevitably be higher than the

average value given in Table 6.4. This is not the whole story, however, because it is yet to be explained why females start from such a high baseline; the intake of cycling females, at 86% that of males, is still "too high", compared to the expected value (according to Kleiber's law) of $(13.38/23.95)^{0.75}=65\%$.

One answer to the problem is that it is perhaps incorrect to view mature females as *ever* being in a non-reproductive state. Despite increasing food intake, lactating females tend to lose body condition (see Chapter 4, and Roberts *et al.*, 1985), and can be expected to have declined to a low point around the time they resume sexual cycling (although there may be some delay between cessation of lactation and resumption of cycling). Figure 4.7 indicates that they then gradually build up condition prior to the next pregnancy, and there is evidence that poor feeding conditions and malnutrition can inhibit ovulation in mammals (Ransom, 1967; Short, 1976). This being so, cycling females will not often be simply maintaining weight, but will be actively increasing it, ecological circumstances permitting, to the point when they can again become pregnant. Males, in contrast, displayed no variance at all in body condition as measured; they always had "perfect" scores of 6. Of course, this ceiling effect does imply a lack of sensitivity inherent in the method of estimating condition, but it also suggests that males were able to maintain a fairly constant weight relative to the fluctuations shown by females. Thus, even cycling females are, in some sense, having to bear energetic costs of reproduction. This may also explain the minimal (and non-

significant) elevation of food intakes in females when they were pregnant. Silk (1986b), however, has made a detailed examination of feeding behaviour in pregnant baboons (*P.cynocephalus*) at Amboseli, finding that time spent feeding increases progressively during pregnancy. It is intended that subsequent analysis of the present data set will involve partitioning reproductive phases, including pregnancy, more finely, thus elucidating whether food intake follows the same trend as feeding time budgets in Silk's study.

(ii) Thermoregulation

Another possible explanation for the apparently small sex-difference in food requirements is that there is some other energetic cost of living which is disproportionately related to body size. One obvious candidate for such a role is thermoregulation. It is well known that homeothermic animals increase metabolic heat production to offset heat loss when the ambient temperature drops below a critical level, and that this critical level is related to body size (e.g. Peters, 1983; Schmidt-Nielsen, 1984). The equation given by Peters (1983) relates the two parameters as:

$$T_{lc} = T_b - 14.6\ W^{0.182}$$

where T_{lc} is the lower critical temperature, T_b is core body temperature (both in degrees centigrade), and W is body weight in kilograms. Body temperatures of baboons at rest are approximately 38° C (Funkhouser *et al.*, 1967). T_{lc} of males and females can therefore be estimated as 11.97° C and 14.59° C respectively. Minimum night-time temperatures at Chololo

ranged between 9-17° C, with an annual mean of 12.33° C. If the conservative assumption that the cut-offs in recorded temperatures were 12° C for males and 14° C for females, females would have spent a part of the night with raised metabolic rates on 317 occasions (87%), whereas males would have done so on only 192 occasions (53%).

The actual frequencies may differ considerably from these estimates, but the calculations serve to emphasize that females would always be more likely to incur thermoregulatory costs. In addition, once below T_{lc}, the increase in metabolic rate required to offset temperature loss is proportionately greater in small animals than in large ones (Peters, 1983). Behavioural thermoregulation can ameliorate physiological costs; the baboons were observed to huddle together on the sleeping rocks, and it is possible that females did so more than males. It would be interesting to know whether high-ranking females have priority of access to the central positions in such clusters, thereby exposing themselves to the minimum heat loss to the environment and the maximum heat gain from neighbouring bodies. This would result in energy balances even more favourable than those suggested simply by the rank-related differences in food intake.

At the other end of the temperature scale, heat stress can also have energetic consequences. Studies have demonstrated the existence of upper critical temperatures (T_{uc} analagous to T_{lc}, above which active metabolic processes aid cooling (Peters, 1983). Funkhouser *et al.* (1976) found that baboons exposed to a temperature of 45° C markedly increased oxygen

consumption after about 60 minutes. Shade temperatures did not reach this level at Chololo (the maximum recorded was 40° C), but temperatures in the sun must have exceeded it considerably (e.g. see Delaney and Happold, 1979; Sharman, 1981). The importance of water availability for thermoregulation, and the impact on the use of shade has already been discussed (Chapter 3), but no mention was made of the energetic implications of heat stress. Unfortunately, no reliable allometric equations describing T_{uc} exist, but there is evidence that, once again, body size is inversely related to the proportional energy costs of thermoregulation at high ambient temperatures. Females could compensate by spending more of their time in the shade, but preliminary analysis of the data does not support this idea; females and males spent 27.4% and 29.1% of their time in the shade respectively. Females spent slightly more time in deep shade than males, but the difference is marginal (4.0% versus 3.3%).

Notwithstanding behavioural strategies, then, the proportional energetic costs of thermoregulation are likely to have been higher for females than for males, and this may have contributed to the relatively high food intakes by former.

(iii) Activities

Did females also expend more energy on activities? This question cannot be fully addressed without extremely detailed information on activity budgets, and some knowledge of the energy costs of each behaviour. These measures are not available in the present case, but some indication can be obtained by comparing the amount of time spent moving (as

opposed to feeding, resting, grooming or other socialising). Males and females spent averages of 33.9% and 34.0% moving, and the difference was not significantly different (correlated t-test, with month as replicator variable; t=0.162, df=6, p=0.876). These data, as far as they go, therefore provide no evidence that females engaged more than males in energetically expensive activity, but, plainly, a more adequate test of the hypothesis would be helpful.

(iv) Diet quality and food intake

Although the subject of age-sex class ecological variability in primates has attracted attention (e.g. Clutton-Brock, 1977; Harrison, 1983) there have been no thoroughgoing attempts to compare diets at the level of chemistry. The 2-way ANOVAs at the beginning of this chapter revealed no differences between reproductive states, including males as a category, in the proportional chemical composition, or in the ratio of protein to fibre, in food ingested. In only one month out of eight was an overall sex difference in diet quality uncovered, when males consumed protein at a higher rate than did females, consequently having superior protein-fibre ratios. These data therefore contradict Demment's (1983) hypothesis that female baboons should have higher-quality, lower-fibre diets than males (see also Chapter 5).

Demment's argument is based on the observation that, while metabolic rate (MR) increases as a fractional power of body weight, gut capacity (GC) increases linearly. Therefore, the ratio MR/GC will be lower in males than in females, allowing males to retain food in their guts longer, and hence to digest

it more completely. Thus, the finding that male and female diets were no different in quality is perhaps surprising; how do females extract sufficient nutrients from food presumably rendered less digestible by their shorter retention times?

It is possible that this problem, and the one of small differences between males and cycling females in food intake, are mutually resolvable. It may simply be easier for females to compensate for the smaller nutritional return they get from each gram of food by consuming relatively large amounts, rather than by searching for higher quality items. Demment's model (*op cit.*) assumes that an inverse relationship exists between fibre content and abundance of foods, and that it pays females more than it does males to concentrate on the rarer low-fibre items. One or both of these assumptions may be incorrect. Firstly, I could find no relationship between phytochemistry and biomass of plant foods (Chapter 5). Secondly, the model does not take account of the potential costs of foraging in a group. Group-living in most primates may be a response to predator pressure (van Schaik, 1983; Dunbar, 1988; c.f. Wrangham, 1980), and baboons are known to be eaten by a number of carnivores, including lions, leopards and hyaenas (DeVore and Hall, 1965; Altmann and Altmann, 1970; Altmann, 1980; Stelzner and Strier, 1981). Individuals are therefore likely to be constrained in their diet choice by the necessity of staying and moving with the group, a point also made by Norton (1986). This may be particularly true for the smaller females, who probably gain protection through keeping close to males (Smuts, 1983, 1985). The roles of different individuals in determining troop

movements among baboons are not yet clear, but it seems that females are certainly not always responsible (Norton, 1986; Strum, 1987). This potentially limits the extent to which females can determine their own foraging paths. Furthermore, the effects of this constraint on female feeding are likely to be exacerbated by competition with males, who are always dominant to females in dyadic interactions (Smuts, 1985; Strum, 1987; personal observations).

The relationship between body size and diet quality is, in contrast, comparatively well documented in the case of interspecific variation (Bell, 1971; Jarman, 1974; Clutton-Brock and Harvey, 1977a; Gaulin, 1979; Sailer *et al.*, 1985). I suggest that, because of the constraints of group foraging, and because there is not necessarily a relationship between food quality and abundance within the range of items utilised by a single species, the intraspecific pattern may frequently differ from the interspecific one. In particular, females may respond to their lesser digestive ability by consuming surprisingly large amounts. In other species, sex differences in diet choice have been found, but no clear pattern emerges in the absence of phytochemical information; *Colobus badius* males were reported to eat more fruit and less foliage than females (Clutton-Brock, 1977), while, in *Cercocebus albigena*, males spent proportionately more time feeding on fruit and less time foraging for insects (Waser, 1977); whether these examples represent cases of divergent ecological strategies or simply competetive exclusion is not known. Van Schaik and van Noordwijk (1986) found that adult male long-tailed macaques (*Macaca fascicularis*) tended to eat larger fruits than adult

females, and suggested that this might be related to protein content, but they also mentioned that strength could have been a constraint. Male orang utans (*Pongo pygmaeus*) studied by Rodman (1977) apparently ate less fruit and more bark than females, and this example fulfils the assumptions of Demment's model rather well; orang utans are highly dimorphic, and they forage solitarily. In addition, bark is clearly a high-fibre and abundant resource compared with fruit.

Other examples of sexually dimorphic diets are given by Clutton-Brock (1977), but these are not easy to interpret. In some cases, differences in body weight may lead to dietary differences through the use of different strata and substrates; in the present study, females spent more time foraging in trees than did males (Chapter 3), but this apparently had minimal impact on dietary composition, probably because males could often feed on flowers and fruits from the ground, either by reaching up and pulling down smaller branches, or by picking up fallen items. In other cases, differences in sheer physical strength may enable the larger sex to exploit foods not available to the smaller one (see also Waser, 1977; p.207; Clutton-Brock, 1977). The large roots of one *Sansevieria* species, which required considerable efforts to extract, were eaten by the male baboons at Chololo, and not by females, but this comprised a very small proportion of the diet (<0.1%).

(iii) Conclusions

Previous studies have tended to emphasize dietary divergence between males and females (see Clutton-Brock, 1977, for a

review). It must be emphasized that I have not demonstrated that there were *no* sex differences in the present case; only the overall feeding rates and chemical composition of diets was examined. The possibility remains to be investigated that differences existed in dietary composition with respect to species and parts of plants eaten. Post (1978) for example, did find that the diets of male and female yellow baboons (*P.cynocephalus*) were distinct, in terms of both composition and overall diversity. I also examined diversity (Chapter 5), but could find no significant difference (though females appeared to differ according to reproductive state). Post (*op. cit.*) suggested that sex differences should be least marked when food abundance is high, because of the reduction in competition, and this may go some way towards explaining the discrepancy in our results. It is worth reiterating, however, that Post's sample consisted of just four individuals, raising the possibility that sex differences and individual differences due to other factors were confounded.

One interesting aspect of the results reported here is the similarity in the daily food intakes of lactating females and of males. Demment (1983) noted that, assuming an increment in basal metabolic rate of about 50% during lactation, females in that state would have quite similar requirements to those of males. He suggested that female body size is limited by the same factors limiting male size, with the addition of the energetic costs of lactation. This perspective is an intriguing departure from the traditional view of the evolution of sexual dimorphism, which emphasizes sexual selection for large size and fighting ability in males

(Da 71; Clutton-Brock *et al.*, 1977; Ralls, 1977; Ale der *et al.*, 1979; Clutton-Brock, 1985). The idea is deserving of further attention, especially in the light of the findings by llner and Martin (1985), which imply that sexual dim phism ates evolved through a process of reduction in fe e, her than by increases in male size. Ecc volutionary implications of size dimorphism are i crse her in Chapter 8.

I have m so suggestions as to why male d cycling fem al s di fered so little in daily food intake. Spe cifically, I argued that the need to regain body condition prior to pregnancy, dispro [illegible] reproductory costs, and low fo d di ity, are all for unexpect intake rly be des p fi ou , or these explanati is cor ect; thi e detailed labo ry s ies of wei s, ergy ntake and ass n, und g regimes of temperature and diet quality, du g each ase of e reproductive cycle.

c) Rank influences female food intake

Understanding the functional significance of dominance relationships amongst female primates, such as those I have described in Chapter 4, is a prerequisite for a proper account of the evolution of sociality (Wrangham, 1980; Dunbar, 1984; van Schaik, 1989). A number of studies have focussed on the nutritional implications of dominance, on the well-founded assumption that, while nutrition limits reproductive success (e.g. Sadleir, 1969; Bongaarts, 1980; Lunn *et al.*, 1984; Lee,

1987), living in groups is likely to give rise to feeding competition (Devore and Hall, 1965; Altmann, 1974; Alexander, 1974; Waser, 1977; van Schaik and van Noordwijk, 1986; Janson and van Schaik, 1988; Dunbar, 1988; van Schaik, 1989). A substantial proportion of the studies on feeding competition which have been done, however, have relied on rather indirect measures of nutrient intake.

The percentage of time spent feeding, in total, and on particular food types, has often been used to measure the nutritional impact of competition between individuals. Altmann (1980) and Post *et al.* (1980), for yellow baboons (*P.cynocephalus*), Wrangham and Waterman (1981) for vervets (*Cercopithecus aethiops*), and van Noordwijk and van Schaik (1987) for long-tailed macaques (*Macaca fascicularis*), found no relationship between overall time spent feeding and dominance rank. However, amongst female yellow baboons feeding at a rubbish dump, a correlation between feeding time and rank was found (Altmann and Muruthi, 1988). In addition, Dittus (1979) for toque macaques (*Macaca sinica*), and Wrangham and Waterman (1981) and Whitten (1983, 1988), for vervet monkeys (*Cercopithecus aethiops*), detected influences of rank on the percentage of time spent feeding on preferred food items.

Individual differences in feeding time budgets are difficult to interpret; it is often assumed that, where feeding time and food intake are correlated, more time feeding will reflect greater food intake (Post *et al.*, 1980; Whitten, 1983; Janson and van Schaik, 1988). Altmann (1980), however, took

the opposite view, assuming that feeding competition would be reflected in a *negative* correlation between feeding time and rank, because low-ranking females were expected to forage less efficiently, and hence compensate by feeding for longer. The only sure way to quantify the effects of competition is therefore to examine the actual intake of nutrients.

Recently there have been a few attempts to do just this. Van Noordwijk and van Schaik (1987) showed that fruit-picking rates by female long-tailed macaques were positively correlated with rank. While overall food intake appeared to be unrelated to rank, high-ranking females acquired their food at less energetic cost. This implies that the effects of competition will sometimes only be revealed when both halves of the energy equation (intake and expenditure) are taken into account. Similarly, Janson (1985, 1988) reported positive correlations between rank and ingestion rates amongst capuchin monkeys (*Cebus apella*).

Van Noordwijk and van Schaik (1987) argue that "in the baboons, feeding on dispersed foods, competition is more likely to be for safe central positions". There may indeed be competition for positions with the lowest risk from predation, but, as is made clear in Chapter 7, these two types of competition are likely to interact. Furthermore, it is evident from the present study that, when the appropriate methodology is used, competition for food is apparent. A general concensus has emerged that the level of intragroup competition is determined by the distribution patterns of resources (Whitten, 1983; Janson, 1985; van Schaik and van

Noordwijk, 1986; Harcourt, 1989). All of these authors argue, and present data to demonstrate, that competition, and hence rank-based differentials, will be most marked where resources are clumped. It appears, then, that at least some of the foods utilised by the baboons at Chololo were sufficiently clumped to elicit competition between individuals, resulting in sizeable differences between high- and low-ranking females in daily intake .

What has not been demonstrated in the present study is that the nutritional advantages of high rank translate into reproductive advantages; this is unavoidable with a short-term study on a large, slow-growing species. That high rank can be associated with enhanced reproduction amongst female primates is evident from other studies. These have been reviewed by Harcourt (1987, 1989), who noted that, in 13 out of 14 studies that have found a difference, dominants either had lower ages at first reproduction or had higher birth rates. Harcourt also noted, however, that most populations which have been studied show no clear difference; for example, during 25 years of intensive study of Old World monkeys, higher reproductive performance in dominant animals has been demonstrated for only five populations.

Harcourt (1989), following Wrangham (1980), and Whitten (1983), suggests that the reason for inconsistency in the relationship between dominance and reproductive success is variation in the degree to which resources are clumped; where food is concentrated in discrete, defensible patches, individuals compete for access, leading to nutritional and

hence ultimately reproductive differences between high- and low-ranking animals (this does, of course, leave open the question of what functional significance dominance relationships have where food is not so distributed - c.f. Dunbar, 1988, and Wasser and Starling, 1988). While Harcourt's argument is plausible, and while there is some evidence to support it (Wrangham, 1981; Whitten, 1983; van Noordwijk and van Schaik, 1987; Altmann and Muruthi, 1988), we still have little knowledge about the nature of the competitive processes underlying rank-based differences. It is this that forms the subject of Chapter 7.

CHAPTER 7: THE DYNAMICS AND SEASONALITY OF FEEDING COMPETITION

1. INTRODUCTION

It was established in the preceding chapter that dominance rank influenced foraging success; high-ranking females ate faster and had higher daily intakes than low-ranking females. While these correlations may reveal something about the functional significance of dominance relations, they do not in themselves tell us much about the actual mechanisms of competition. In this chapter I am concerned with the way in which the competitive process operates through social interaction and patterns of spatial deployment.

Recently, a distinction has been made between "contest" and "scramble" modes of feeding competition in primates, which can occur between individuals within groups, or between groups (Post, 1978; Janson and van Schaik, 1988; following Nicholson, 1954). Within-group contest competition "occurs when aggression or displacements between group members lead to reduced food intake for some individuals...(whereas)...within group...scramble competition is the result of some individuals removing limited food supplies from an area before other group members have a chance to feed" (Janson and van Schaik, *op cit.*). It seems likely that there will often be a mixture of these two modes, their relative importance being determined by the spatial distribution of particular resources. Janson and van Schaik (*op cit.*) state that within-group contest

competition has no discernible effect in baboons (citing Post *et al.* (1980), a reference which has also been used - by Wrangham, 1983 - to argue the reverse!), but this is evidently not true in the present case, and it is this type of competition which I focus on here.

While, in certain circumstances, contest competition may be manifested in overt aggressive interactions (e.g. Klein and Klein, 1975; Dittus, 1977; Janson, 1985; Belzung and Anderson, 1986), in others, the mechanisms of resource partitioning may be more subtle, involving the avoidance of direct confrontation, and discernible only by observation of patterns of a group's spatial organisation (Robinson, 1981; Sugiyama and Ohsawa, 1982; Furuichi, 1983; Belzung and Anderson, 1986; van Noordwijk and van Schaik, 1987). Whitten (1983) found that the rates of aggressive supplants by vervet monkeys (*Cercopithecus aethiops*) did not reflect variation in the intensity of competition for between different foods, or between different groups. It is therefore of value to determine how individuals differ in the spatial locations that they take up spontaneously, out of "respect" (sensu Kummer *et al.*, 1978) for the ownership by dominant animals of particular positions or feeding sites.

2. COMPETITION AND SPATIAL DEPLOYMENT: AN EXPERIMENT

In January 1986, while I was habituating the indigenous baboon troop prior to detailed data collection, an opportunity arose to conduct an intensive short-term study of the social

dynamics of feeding competition amongst females in a provisioned group. The group, known as Malaika (MLK), had been translocated to the study area in September 1984, and was highly habituated (see Chapter 2 for further details). Due to the low rainfall over the preceding months, and the consequently poor feeding conditions, these animals, unlike their indigenous counterparts, were failing to find enough natural foods to survive, and some were near starvation. The decision was therefore taken by the director of the site to provision them temporarily, to tide them over until conditions improved.

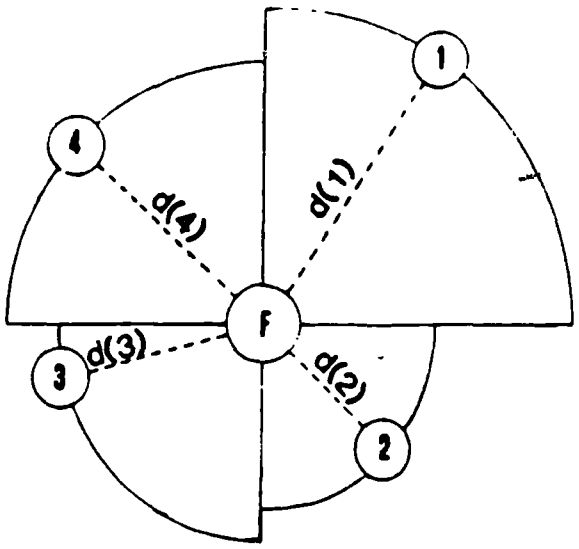
Each morning for about two weeks, cubes of "monkey chow" were scattered over a small area of about 15 metres in diameter, close to the sleeping rocks. Although formal measurements were not made, it was clear that these artificial patches contained a density of food far greater than any of the natural foods within the animals' home range. Furthermore, the patches were small enough such that the whole troop could not be easily accommodated, and relatively high levels of aggression were immediately observed. The baboons would gather round, and feed avidly for about 90 minutes, until all the cubes had been eaten.

These artificial conditions seemed ideal for an analysis of the social processes mediating competition. It is highly probable that interaction rates and the effects of competitive exclusion would be elevated above the usual levels in the natural situation, as has been found in provisioned *Macaca fuscata* (Sugiyama and Ohsawa, 1982), and in baboons feeding at

a rubbish dump (Altmann and Muruthi, 1988). If intragroup contest competition is a significant feature of baboons (which the preceding chapter indicates it is), then it should certainly be discernible under such conditions. There is no reason to suppose, however, that *qualitatively* abnormal patterns of behaviour would arise. Indeed, the situation closely resembled that observed amongst the indigenous troops at "corming" sites, which were also spatially concentrated food sources (see sections 3-5, below). Another advantage of the artificial situation was that the whole troop was in view, allowing the use of measures of spatial deployment not otherwise possible. Subsequently, the cubes were scattered over a wider area in order to reduce competition and allow low-ranking animals to feed more easily, so the study was restricted to the initial two-week period.

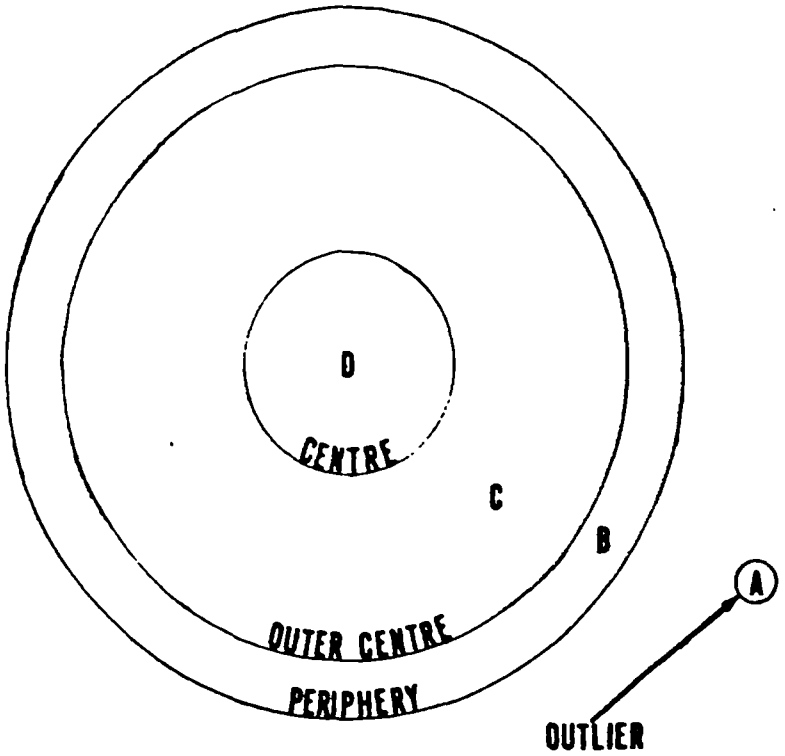
Each of the nine adult females in the group were sampled. Individuals' food ingestion rates and rates of supplanting and being supplanted were measured continuously, as described for the rest of the study. In addition, I employed two measures of spatial positioning (Figure 7.1). The proximity index (PI) estimates the area of unoccupied space surrounding the focal animal, calculated as the sum of the areas circumscribed by the distance to the nearest neighbour in each of four quadrants surrounding the focal animal. The centre-periphery index (CPI) is a measure of the focal's location within the troop, and is calculated as the weighted sum of frequencies of occupation of four radial zones, divided by the total number of instantaneous samples; the innermost circle is weighted by multiplying frequencies by four, the middle segment is

A



$$P.I. = \sum_{1,4} \frac{\pi d_n^2}{4}$$

B



$$C.P.I. = \frac{n_A + 2n_B + 3n_C + 4n_D}{n_A + n_B + n_C + n_D}$$

FIGURE 7.1: MEASURES OF FOCAL'S SPATIAL POSITION IN TROOP. A - The Proximity Index, which estimates the area of unoccupied space surrounding F, the focal animal, with reference to the nearest neighbour in each of four quadrants. B - The Centre-periphery Index, a measure of the location of the focal animal within the troop.

multiplied by three, and so on. The PI has some resemblance to a "domain of danger" spatial measure developed independently by Busse (1984) in his study of chacma baboons (*P.ursinus*), while the CPI is similar to measures of centrality used by Robinson (1981) on capuchin monkeys (*Cebus nigrivittatus*), Collins (1984) on yellow baboons (*P.cynocephalus*), and Waser (1985) on mangabeys (*Cercocebus albigena*). Both measures were recorded as an instantaneous sample every 30 seconds.

The duration of focal samples was fixed at ten minutes, so that each of the nine adult females in the group could be sampled once within each provisioning episode. Clearly it is to be expected that ingestion rates would decline as the cubes were depleted, so it was important to ensure that the sampling order was unbiased. Accordingly, I generated a sampling order randomly (by picking names out of a bag); the order was varied by moving one place down the order each day, such that the second individual from the previous day was sampled first, and the first individual from the previous day was sampled last. Samples were collected on nine days; thus the rotating order ensured that each female was sampled once in each position, yielding ninety minutes of samples per individual. Although the dominance ranks of all the females in the group were being monitored by Dr. Strum's research group, they were not made known to me until after completion of the study.

Table 7.1 displays correlations amongst ingestion rates, spatial measures, supplant rates and dominance rank. Firstly, mean ingestion rate is positively correlated with dominance

rank, replicating the findings of the previous chapter for the natural situation. Secondly, both the spatial measures are also highly correlated with dominance rank; the negative correlation for PI indicates that high-ranking females (HRFs) had smaller areas of unoccupied space around them, while the positive correlation for CPI indicates that HRFs showed a strong tendency to occupy the central positions in the group. Associations with supplant rates are weaker, being significant only in the case of the negative correlation between rank and the rate of receiving supplants. The overall supplant rate was quite low, there being on average one event every 2.22 minutes.

TABLE 7.1: CORRELATIONS AMONGST RANK, FOOD INTAKE, SPATIAL MEASURES AND SUPPLANTING

	RANK	INGESTION RATE
INGESTION RATE	0.783^{*}	-----
SPATIAL MEASURES		
a. PROXIMITY INDEX	-0.917^{***}	0.800^{**}
b. CENTRE-PERIPHERY INDEX	0.863^{**}	0.742^{*}
SUPPLANT RATES		
a. GIVE SUPPLANTS	0.122	0.140
b. RECEIVE SUPPLANTS	-0.709^{*}	-0.658
c. GIVE/RECEIVE RATIO	0.051	0.026

Notes: Tabulated values are Spearman rank correlation coefficients. *** p<0.001 ** p<0.01 * p<0.05, DF=7.

The spatial measures appear to show the strongest associations with food intake, while also being highly correlated with rank. This perhaps suggests that intake was determined proximately by the spatial positions of individuals, which were in turn determined by rank, rather than rank having a direct effect on intake. The idea could be tested by

examining the relationship between spatial measures and ingestion rate, with the effect of rank partialled out, and conversely, the relationship between rank and ingestion rates with spatial measures partialled out. Strictly, a nonparametric test should be used, since one of the variables consists inherently of rank-order data. Unfortunately, the sampling distribution is unknown for the only nonparametric partial correlation method that exists (Siegel, 1956). I have therefore relaxed usual distributional assumptions, and used parametric partial correlations to give an idea of the pattern of associations. The correlation between ingestion rate and rank is not significant when the effects of either the CPI or the PI are partialled out (partial r_{cpi}=0.223, df=6, p=0.298: partial r_{pi}=0.071, df=6, p=0.434). Conversely, when the effect of rank is partialled out, the correlations between ingestion rate and spatial measures are higher, being significant for PI (partial r_{rank}=$^{-}$0.703, df=6, p=0.026), though not for CPI (partial r_{rank}=0.356, df=6, p=0.194).

Did supplants play any role in regulating spatial position? Table 7.2 shows that only the rate of receiving supplants was significantly correlated with the spatial measures, and that even this association disappears when the effect of rank is partialled out. It is important to remember, however, that supplants may be used primarily when the group first encounters a patch, as dominant animals establish their positions. Thereafter, assuming that dominance relations are clear-cut, subordinates would do better to avoid direct conflicts, so as not to waste energy or risk injury when the probability of obtaining food was low. Under these

FIGURE 7.2: RELATIONSHIP BETWEEN SUPPLANT RATE AND ELAPSED TIME FROM START OF PROVISIONING (Data points are means for 5-minute blocks)

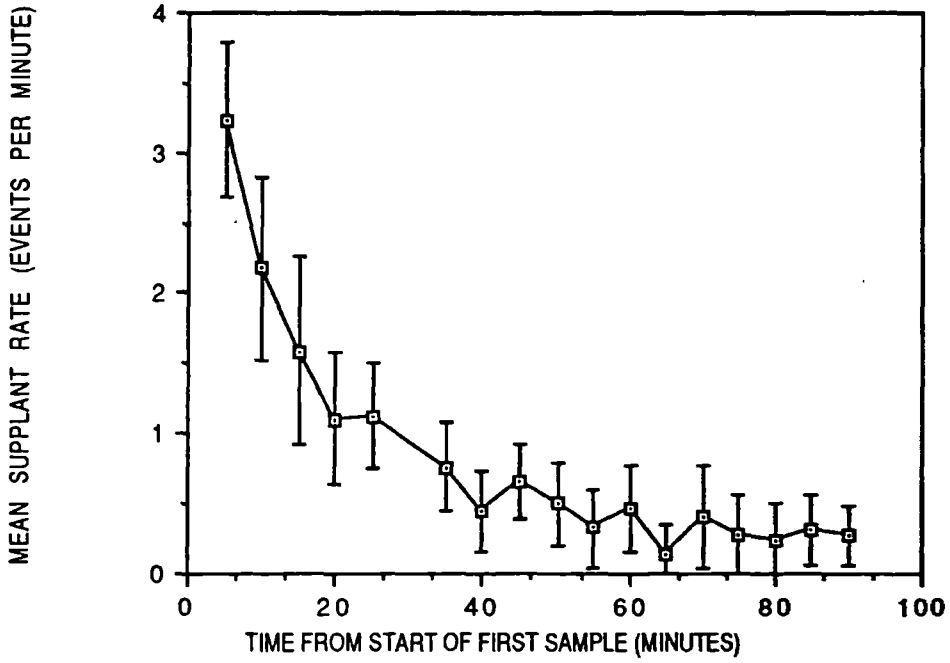


TABLE 7.2: CORRELATIONS BETWEEN SUPPLANT RATES AND SPATIAL MEASURES

			PARTIAL RANK	
	PI	CPI	PI	CPI
SUPPLANT RATES				
a. GIVE	-0.227	0.172	-0.373	-0.123
b. RECEIVE	0.819**	-0.690*	0.204	-0.117
c. GIVE/RECEIVE RATIO	-0.269	0.225	-0.187	-0.389

Notes: ** $p<0.01$ * $p<0.05$, df=7 for zero-order correlations, df=6 for partial correlations.

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conditions, then, we would expect to observe a relatively high rate of supplants initially, followed by a period during which spatial deployment patterns were maintained primarily by avoidance by subordinates. This is confirmed by examination of the changes in supplant rates over time (Figure 7.2).

Thus the evidence suggests that the proximate determinant of food intake was spatial location within the troop, which was itself related to rank. The correlations indicate a "dominance gradient", with the highest-ranking females at the centre of the troop, monopolising access to the best feeding sites, and the lowest-ranking females at the periphery. The lower PIs of high-rankers was presumably a direct reflection of their centrality. Aggressive supplants appeared to play little direct role in regulating spatial deployment. These findings will later be discussed in relation to patterns of competition in the natural setting, which are described below.

3. SEASONAL VARIATION IN THE INTENSITY OF COMPETITION

Because of relatively poor visibility during observations in the natural situation, I was unable to employ either of the spatial measures used in the provisioning study. Instead, I recorded the number of individuals within a 10-metre radius of the focal animal (excluding dependent infants), at every point-sample. Although I recorded this whatever the activity of the animal, for the purpose of these analyses I include only point-samples in which it was feeding. This measure is used together with rates of supplanting, to evaluate the intensity and nature of competition in each month of the study period. The rationale is as follows: having a large number of neighbours while feeding should reflect a relatively high level of competition; such clustering could be due to the use of clumped resources, to increased risk of predation at certain times of year, or to both. Similarly, while it is possible that supplanting is not an important strategy for getting food, any variation in rates is nevertheless likely to be related to the degree to which individuals are clustered. Because feeding supplant rates were low (mean = 1 supplant every 29.9 minutes of feeding time), there were insufficient data to permit analyses broken down by both individual and month, as was possible for the number of neighbours data.

Previous studies have found that the number of individuals in close proximity to a female baboon, and her spatial location with respect to the group, are influenced by her reproductive state (Rowell, 1969, 1972; Rhine, 1975; Seyfarth, 1976; Altmann, 1980; Collins, 1984). The former statement is supported in the present case; a two-way analysis of variance

was performed, revealing that the mean number of neighbours differed significantly according to both reproductive state (excluding males) and month (Table 7.3). Lactating females had the highest average (2.61), followed by cycling females (2.49) and pregnant females (2.37). It is therefore not surprising that the mean number of neighbours for each focal female during the study period is positively correlated with the percentage of months spent lactating ($r=0.512$, $df=16$, $p=0.024$).

TABLE 7.3: RESULTS OF TWO-WAY ANOVA TO INVESTIGATE THE EFFECTS OF REPRODUCTIVE STATE AND MONTH ON THE NUMBER OF NEIGHBOURS (FEMALES ONLY).

	F-RATIO	DF	P
MAIN EFFECTS	5.148	9	<0.001
REPRODUCTIVE STATE	5.196	2	0.007
MONTH	6.156	7	<0.001
INTERACTION	1.265	14	0.240

These results accord with previous findings that female baboons with young infants are particularly attractive to other group members (De Vore, 1963; Rowell *et al.*, 1968; Seyfarth, 1976; Altmann, 1980), and tend more than cycling and pregnant females to be found near the centre of the group (Busse, 1984; Collins, 1984), while pregnant females are the least socially active and most peripheral class (Saayman, 1971b; Rowell, 1972; Collins, 1984). It is obvious therefore, that characteristics of the resource being exploited are not the only influence on the number of neighbours, and that analysis of seasonal variation should control for the effects of reproductive state.

Monthly variation in the mean number of neighbours within ten metres while feeding is presented in Figure 7.3., and variation in overall supplant rates is shown in Figure 7.4., both calculated as the mean of values for each reproductive state. Variations in these two parameters are not significantly correlated ($r=0.341$, $df=8$, $p=0.336$).

One of the ecological conditions specified by Wrangham (1980) in his model of female-bonded primate groups is that, during periods of scarcity, a switch to foods occurring in large, low-quality patches should occur, allowing individuals to spread out and reduce competition with other group members. The opposite appears to obtain in the present case. Firstly, number of neighbours and supplant rate are negatively, not positively, correlated with biomass and rainfall, although only one of the correlations is significant (Table 7.4).

TABLE 7.4: CORRELATIONS BETWEEN ENVIRONMENTAL PARAMETERS AND NUMBER OF NEIGHBOURS AND SUPPLANT RATE

		RAINFALL IN MONTH:		
	FOOD BIOMASS	SAME	PREVIOUS	SAME+PREVIOUS
NEIGHBOURS	$^{-}0.556$	$^{-}0.345$	$^{-}0.583$	$^{-}0.538$
SUPPLANT RATE	$^{-}0.631$	$^{-}0.286$	$^{-}0.730^{*}$	$^{-}0.594$

Notes: * $p<0.05$, $df=6$ for biomass, $df=8$ for rainfall.

Secondly, collapsing the monthly number of neighbours data into two categories, wet months and dry months, and performing a two-way ANOVA similar to the one above, shows that the mean

FIGURE 7.3: MONTHLY VARIATION IN MEAN NUMBER OF NEIGHBOURS WHILE FEEDING

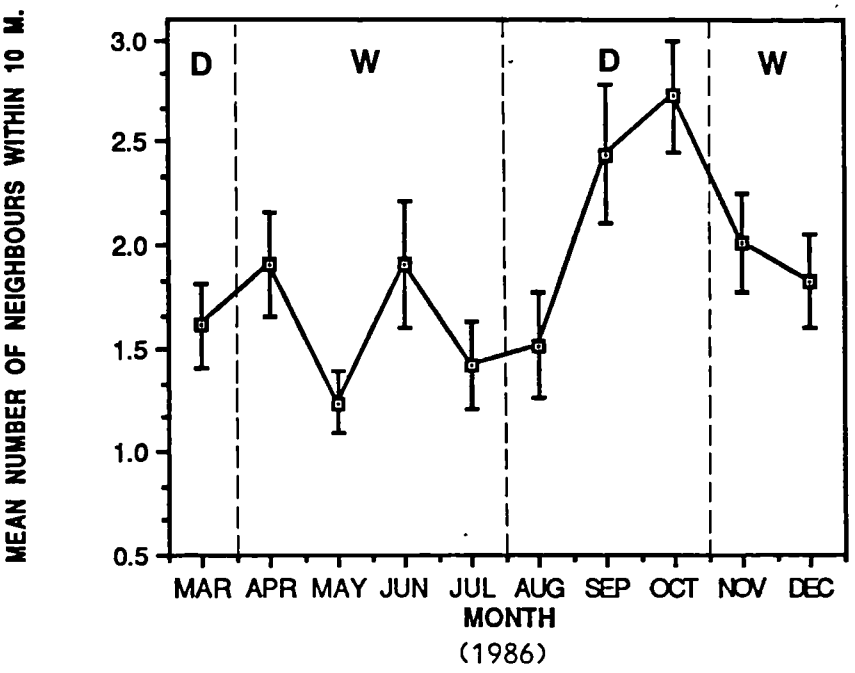
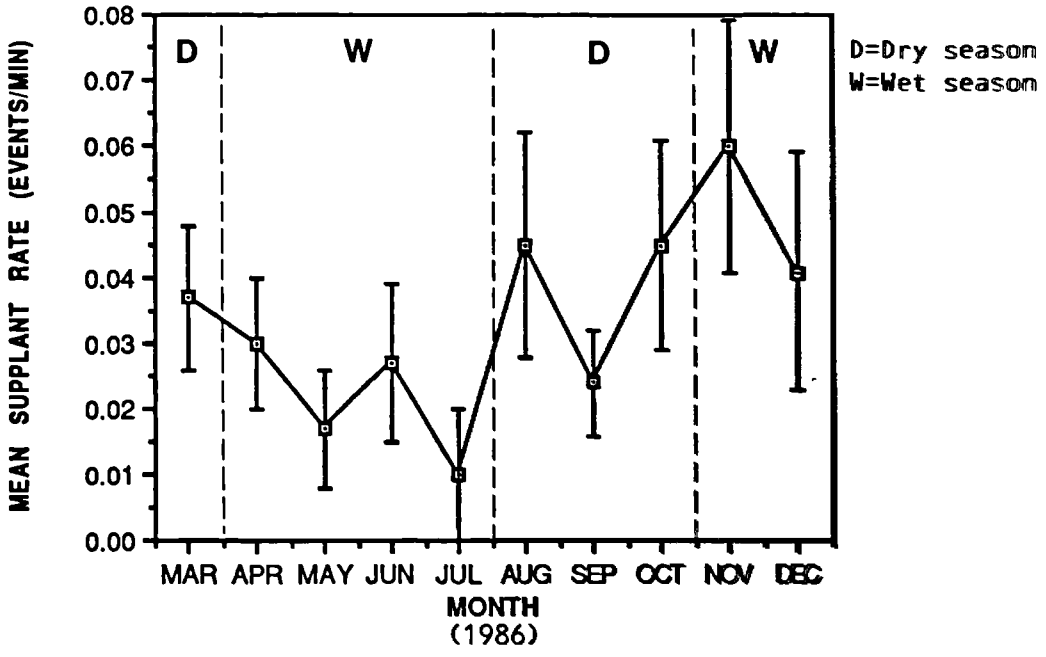


FIGURE 7.4: MONTHLY VARIATION IN MEAN SUPPLANT RATE



was significantly higher in the dry season than in the wet season ($F=13.176$, $df=1$, $p<0.001$; mean dry season = 2.13, mean wet season = 1.73; Tukey test, $Q=4.823$, $p<0.001$). The same type of analysis cannot be performed on supplant rates, as explained above, but the mean was again higher in the dry season than in the wet (2.49 per hour versus 1.51 per hour), and a t-test on these data indicates a significant difference ($t=2.31$, $df=8$, $p=0.050$).

It has already been suggested that the intensity of competition will be related to the spatial distribution of the resource being exploited, and we might expect to find correlations between the mean number of neighbours or supplant rate, and the monthly percentage of feeding time devoted to clumped foods versus dispersed foods. As discussed in Chapter 3, objective measures of clumping on a scale relevant to the behaviour of the animals being studied are difficult to acquire. Subjectively, it seemed reasonably clear that corms of the sedge *Cyperus blysmoides*, and some *Acacia* products, occurred in dense patches with limited feeding sites (see discussion in Chapter 3). Table 7.5 shows that, in each of these cases, feeding time was correlated with one, but not both, measures of competition. Feeding time on other food types, however, showed no significant correlations.

In conclusion, the observed variation in the degree to which the baboons fed in clusters and in the rates at which feeding supplants occurred, suggests that the level of contest competition was higher in the dry season, when food was relatively scarce. This was probably due to an increased

TABLE 7.5: CORRELATIONS BETWEEN TIME SPENT FEEDING ON MAJOR FOODS AND MEAN NUMBER OF NEIGHBOURS AND SUPPLANT RATE

	N NEIGHBOURS	SUPPLANT RATE
PERCENTAGE OF FEEDING TIME		
Acacia flowers	0.840***	0.216
Acacia pods	0.123	0.481
C.blysmoides corms	0.283	0.552*
Sedge bases	0.065	0.238
Foliage	-0.472	-0.001
Fruit	-0.435	-0.348
Euphorbia stems	-0.098	0.003

Notes: *** $p<0.001$ * $p<0.05$, df=8.

tendency for food to be concentrated in relatively discrete, monopolisable patches at this time. In the following section, I examine further the relationship between resource characteristics and the intensity of competition.

4. THE INFLUENCE OF FOOD QUALITY AND DISTRIBUTION

Optimality theory (e.g. MacArthur and Pianka, 1966; Krebs, 1978) implies that individuals should adjust their energetic investment in contest competition according to the net return from each resource. We may therefore predict that the intensity of competition for each food will be related to its quality, in terms of both chemical composition and relative local density (degree of "clumpedness"). In the light of diet selection principles elucidated in Chapter 5, we may further specify that competition is expected to be strongest for foods which are high in protein and low in fibre.

Empirically, however, there is already reason to doubt that the prediction of an association between phytochemistry and the intensity of competition will be confirmed; high-ranking females had greater daily intakes, but not better-quality diets. Because of this, we may predict that the spatial distribution of foods is the primary determinant of the levels of competition they evoke. Unfortunately, as explained above, no meaningful quantitative measures of clumping or of patch size are available. Therefore, in the following correlational analysis of relationships between competition and resource characteristics, measures of the latter include only chemical composition and dry weight ingestion rate. Shopland (1987) performed a similar analysis, and also encountered the problem of quantifying food distribution. Her solution was to class food types as either clumped or uniformly distributed, on a scale appropriate to groups of foraging baboons:

" A food was considered clumped if it was distributed in patches that could accommodate several baboons but not the whole group, and within which the density of food units was high...A food was scored as uniformly distributed if it occurred in large stands that could accommodate the entire baboon group without crowding: the density of food units within the stand could be high or low" (Shopland, 1987).

Note that Shopland's dichotomy actually concerns "patch size" as much as it does general spatial heterogeneity. In the absence of any obvious improvement on this method, I have adopted the same procedure, and I have retained her terminology for convenience. According to this definition, six foods for which sufficient data were available were scored as clumped: *Cyperus blysmoides* corms, *Acacia tortilis* flowers, *Acacia etbaica* flowers (but only those collected from drifts on the ground; flowering trees themselves often occurred in large groves), *Acacia nilotica* pods, *Acacia*

mellifera pods, and *Euphorbia nyikae* fleshy stems. A seventh food type, *Lycium europaeum* leaves, was difficult to classify, and so was excluded from the analysis.

A comparison of clumped versus dispersed foods shows that both the mean number of neighbours and the mean supplant rate were greater when animals were feeding on the former (number of neighbours; $t=4.19$, $df=23$, $p<0.001$: supplant rate; $t=2.24$, $df=23$, $p=0.032$), indicating a link between resource distribution and the intensity of competition. A problem with the procedure, however, is that clumped foods were also foods obtained from trees in 3 out of the 5 cases, whereas non-clumped foods were obtained from trees in only 2 out of 22 cases; this means that "clumped food" and "three-dimensional substrate" are confounded. There is no clear reason in principle to expect supplant rates to be higher in a three-dimensional situation, but clearly the number of neighbours are likely to be greater, without any concomitant increase in the level of competition, because of the greater number of feeding sites per square metre. Comparing tree foods and non-tree foods, number of neighbours were significantly greater for the former ($t=4.57$, $df=24$, $p<0.001$), whereas, as predicted, there was no difference in supplant rate ($t=0.17$, $df=24$, $p=0.870$).

The present data set does not permit a rigorous separation of the influences of these factors on the number of neighbours, because there were only two clumped non-tree foods. However, in the case of one of the latter, *Cyperus blysmoides* corms, both the mean number of neighbours (7.9) and the mean supplant

rate were greater (0.231 per minute) than for any other food. In the case of fallen *Acacia etbaica* flowers, the other clumped non-tree food, the two parameters were also relatively high (4.4 neighbours and 0.057 supplants per minute, compared with the mean for all clumped foods of 4.7 neighbours and 0.085 supplants per minute, and means for all non-clumped foods of 1.6 neighbours and 0.032 supplants per minute). Conversely, for the two non-clumped tree foods, the numbers of neighbours were fairly high, while supplant rates were low (number of neighbours; 2.8 and 4.6: supplant rates; 0.026 and 0.011: foods are pods of *Acacia seyal* and *A.mellifera* respectively). Thus, the available evidence does suggest that, while spatial deployment was influenced by the use of arboreal versus terrestrial sources of food, it was also independently influenced by the degree to which foods were clumped, whereas supplant rates were influenced only by the latter.

Next I turn to the relationship between chemical composition and the intensity of competition. In order to control for the effects of food distribution and substrate, I have excluded the 9 foods which were either clumped or obtained from trees. Correlations are displayed in Table 7.7; none are significant. Number of neighbours and supplant rate are, however, significantly correlated with each other ($r=0.514$, $df=25$, $p=0.008$), suggesting that they do indeed reflect aspects of the same underlying behavioural process.

TABLE 7.7: CORRELATIONS BETWEEN FOOD CHEMISTRY AND NUMBER OF NEIGHBOURS AND SUPPLANT RATE

		PERCENTAGE DRY WEIGHT				
	YIELD	PROTEIN	FIBRE	P/F	TANNINS	RESIDUAL
N NEIGHBOURS	0.277	-0.230	-0.187	-0.302	0.093	0.375
SUPPLANT RATE	0.240	0.099	0.124	0.037	-0.063	-0.191

Notes: Yield = ingestion rate in grams dry weight per minute.
All correlations non-significant

Were the foods evoking the highest levels of competition also those which showed rank differences in consumption? Sufficient data are available for analysis of 19 foods (where "sufficient data" is defined as at least five bouts of feeding recorded for each of the adult females). Of these 19 foods, there were positive correlations between rank and ingestion rate in 16 cases, though only four reached significance (Table 7.8). Both the mean number of neighbours and mean supplant rate were significantly greater for these four foods (number of neighbours; $t=3.36$, $df=17$, $p=0.004$: supplant rate; $t=3.33$, $df=17$, $p=0.004$), thus demonstrating that rank-related effects on intake were most marked for the foods which evoked high levels of direct competition. It should also be noted that three out of the four foods showing significant rank-related effects were principally dry season foods (blades of *P.mezianum* being the exception), reinforcing the conclusion of section 7.2 that competition tended to be greater in the dry season than in the wet season.

TABLE 7.8: CORRELATIONS BETWEEN DOMINANCE RANK AND INGESTION RATE, AND MEAN NUMBER OF NEIGHBOURS AND SUPPLANT RATE, FOR 19 FOODS.

FOOD	1	2	3
Acacia etbaica flowers (tree)	0.514*	3.80	0.019
Acacia etbaica flowers (ground)	0.456*	4.38	0.027
Acacia tortilis flowers (tree)	0.199	4.40	0.022
Commelina erecta buds	-0.252	0.85	0.000
Cynodon dactylon blades	0.288	1.86	0.034
Cynodon plectostachyus blades	0.197	1.63	0.009
Cyperus blysmoides corms	0.611**	7.86	0.231
Cyperus merkeri bases	-0.029	1.84	0.030
Ipomoea mombassana fruits	0.050	1.47	0.090
Lycium europaeum leaves	0.253	1.81	0.037
Mariscus amauropus bases	0.139	0.99	0.017
Osteospermum vaillantii fruits	0.147	0.59	0.034
Penissetum mezianum blades	0.509*	2.67	0.046
Penissetum spp. blades	0.442	1.18	0.000
Sansevieria intermedia bases	-0.204	0.98	0.032
Trachyandra saltii leaves	0.230	1.23	0.018
Tragus bertoriana inflorescences	-0.252	1.54	0.020
Tribulus terrestris leaves	0.418	1.69	0.018
Tribulus terrestris fruits	0.206	2.28	0.012

Notes: 1; pearson correlation coefficient between rank and ingestion rate (** $p<0.01$, * $p<0.05$, df=16). Foods included are those for which 5 or more feeding bouts were recorded for each female.
2; mean number of neighbours within 10 metres.
3; number of supplants per minute.

5. DOMINANCE RANK, SPATIAL DEPLOYMENT AND SUPPLANTING

The evidence of section 7.2 suggested that the nutritional advantages of high rank in a provisioned group were mediated by spatial deployment, with supplants apparently being of little direct importance. In this section I evaluate whether the tendency of high-rankers to occupy central positions, or to otherwise monopolise feeding sites, was also a feature of

the naturally-foraging group. Two parameters are examined here: the number of neighbours, as a surrogate for the proximity index, and the use of trees, which simplifies the definition of patches. Finally, correlations between dominance rank and supplant rates are presented.

(a) Number of neighbours

If high-ranking females (HRFs) monopolise the best feeding sites within patches, and thus tend to occupy central positions in a way similar to HRFs in the provisioned group, this is likely to be reflected in the number of animals in close proximity to them while feeding. I have collapsed data for individual females into three rank categories, high medium and low, and performed a one-way repeated measures ANOVA, with food type as the replicator variable. This procedure reveals that the number of neighbours differed significantly between rank categories ($F=3.372$, $df=2,38$, $p=0.045$: means; high=2.05, medium=1.79, low=1.58), with high-rankers having significantly more than low-rankers (Tukey test: $Q=3.642$, $p=0.037$).

To pursue the influence of dominance further, and to investigate the possibility that the effect is due simply to the tendency for HRFs to be more attractive (Seyfarth, 1977; Gouzoules and Gouzoules, 1986; Walters and Seyfarth, 1986), or to have larger families (Sade *et al.*, 1976; Silk, 1986a), I compare the influence of rank during feeding with that during other activities; if effects during feeding, but not during other activities, are apparent, this would support the

idea that differences were due directly to competition for feeding sites, rather than to attractiveness or family size.

Correlations between rank and the number of neighbours within 10 metres, broken down by food type, are displayed in Table 7.9. All of the 10 correlations are positive, with three being significant, indicating that HRFs tended to have more close neighbours when feeding than LRFs did. Rank was, however, uncorrelated with the number of neighbours in the other major activities (moving; $r_s=^-0.091$, p=0.710: standing; $r_s=^-0.089$, p=0.716: resting; $r_s=0.119$, p=0.627: grooming; $r_s=^-0.004$, p=0.988: df=17 in each case).

TABLE 7.9: CORRELATIONS BETWEEN RANK AND THE NUMBER OF NEIGHBOURS, BROKEN DOWN BY FOOD TYPE

FOOD	r_s
Acacia etbaica flowers (tree)	0.47*
Acacia etbaica flowers (ground)	0.03
Acacia tortilis flowers (tree)	0.15
Cynodon dactylon blades	0.18
Cyperus blysmoides corms	0.61**
Euphorbia nyikae fleshy stems	0.46*
Lycium europaeum leaves	0.32
Mariscus amauropus bases	0.19
Tragus bertoriana inflorescences	0.24
Tribulus terrestris fruits	0.14

Notes: tabulated values are Spearman's rank correlation coefficients (* p<0.05, df=16). Foods included are those eaten in >5 point samples by each female.

(b) Use of trees

I have suggested that the nutritional advantages enjoyed by high-ranking females are likely to be mediated by priority of access to feeding sites or patches containing relatively high densities of food. What evidence is there for this? Whilst

there is frequent talk in primate behavioural ecology of the significance of "patches", in practice, these phenomena are extremely difficult to define, let alone to measure (Wrangham, 1983), and no attempt was made in the present study to do so. Trees, however, are a class of patch which it is relatively easy to measure and delineate the boundaries of. Accordingly, in this section I evaluate the evidence that HRFs had priority of access to foods obtained from trees.

Animals sometimes fed on tree products by reaching up from the ground, but this appeared to be less efficient than when they climbed into the tree. This subjective impression can be tested by comparing the feeding rates of individuals when they were in trees with their feeding rates when outside the tree. In the case of *A.etbaica*, feeding rates were significantly higher when individuals were in trees than when they were outside them (correlated t-test, individual as replicator variable; t=2.59, df=18, p=0.019, means = 49.3 and 44.7 bites per minute respectively); in the case of *A.tortilis* there was no significant difference (t=1.21, df=12, p=0.250, means = 47.6 and 50.5 bites per minute), but the number of non-tree bouts recorded for each individual is small (mean=2.7), so the test is not very reliable. In general, then, feeding on *Acacia* flowers was less efficient when individuals harvested them from a terrestrial position. The next question is whether there were rank-related differences in the extent to which individuals fed in and out of trees.

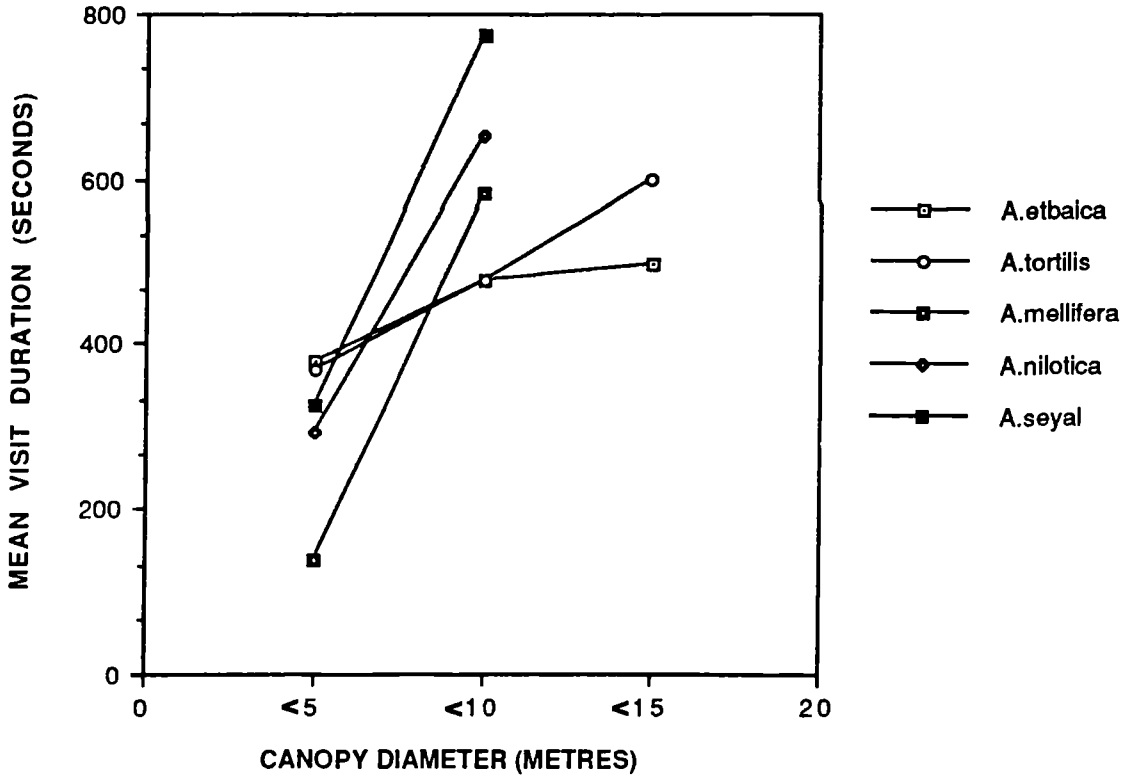
Unfortunately, there are insufficient data to analyse trends for the two *Acacia* species separately, so I have pooled the

data. While rank is uncorrelated with the overall percentage of time spent in *Acacia* trees (r_S=⁻0.185, df=16, p=0.464), there is a significant positive correlation between rank and the proportion of feeding time on *Acacia* flowers that was spent actually in the tree, as opposed to picking the flowers from a position on the ground (r_S=0.472, df=16, p=0.048). The same type of analysis cannot be performed on any other tree species, due to a lack of data, but the same trend is apparent in the context of feeding on *Euphorbia nyikae* fleshy stems; high-rankers spent 63.5% of their feeding time on this item actually in the tree, while for medium-rankers the figure is exactly 50%, and for low-rankers 0%.

Acacia trees utilised by the baboons varied substantially in size; each time the focal animal climbed into a tree I estimated the canopy diameter as being less than 5 metres, 5-10 metres, 10-15 metres, or 15-20 metres. Figure 7.5 clearly shows that, for a number of *Acacia* species, the duration of feeding visits to trees, and hence presumably patch richness, was a positive function of crown diameter. This suggests that crown diameter may be used as an index of patch quality; did HRFs monopolise the larger trees?

Figures 7.6 and 7.7 display the average percentages of feeding time spent in *A.etbaica* and *A.tortilis* that was allocated to different sizes of tree by high-, medium-, and low-ranking females. In the case of *A.etbaica* there appears to be a clear relationship between rank and the size of trees selected, with HRFs feeding more in larger trees. No such relationship is apparent for *A.tortilis*, however. In Figure 7.8 I have

FIGURE 7.5: RELATIONSHIP BETWEEN CANOPY DIAMETER AND DURATION OF VISITS TO ACACIA TREES



Duration of visits = time in seconds between entering and leaving tree.

FIGURE 7.6: RELATIONSHIP BETWEEN RANK AND THE SIZE OF A.ETBAICA TREES OCCUPIED

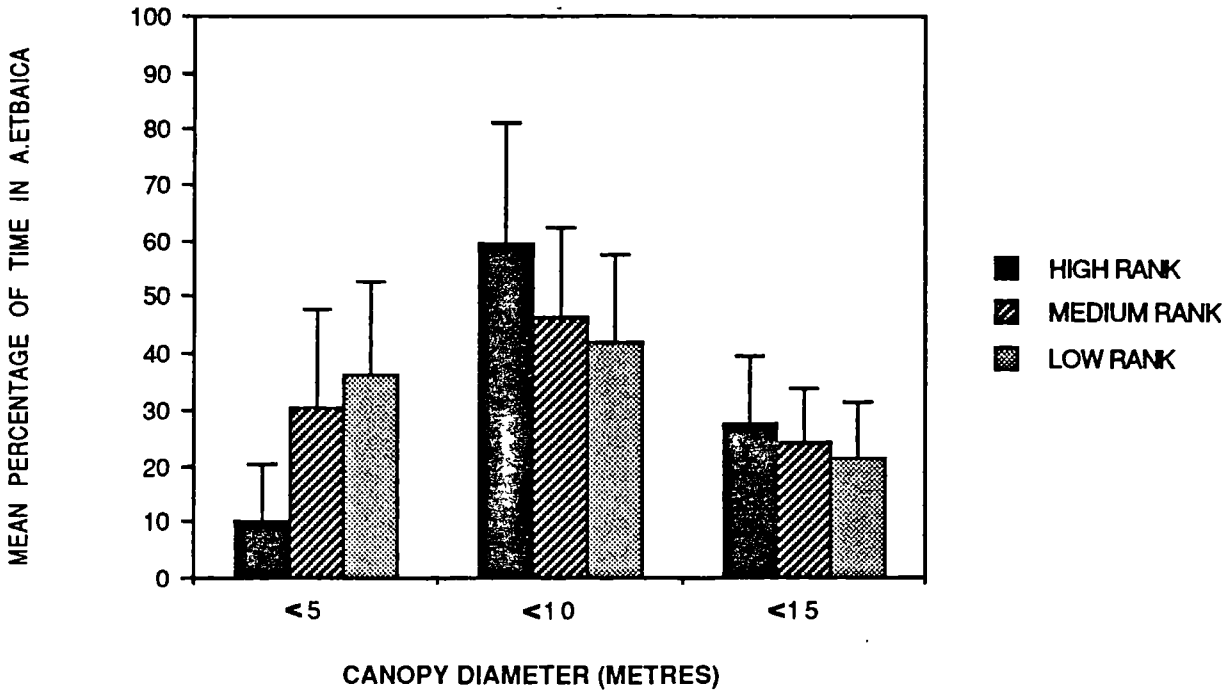
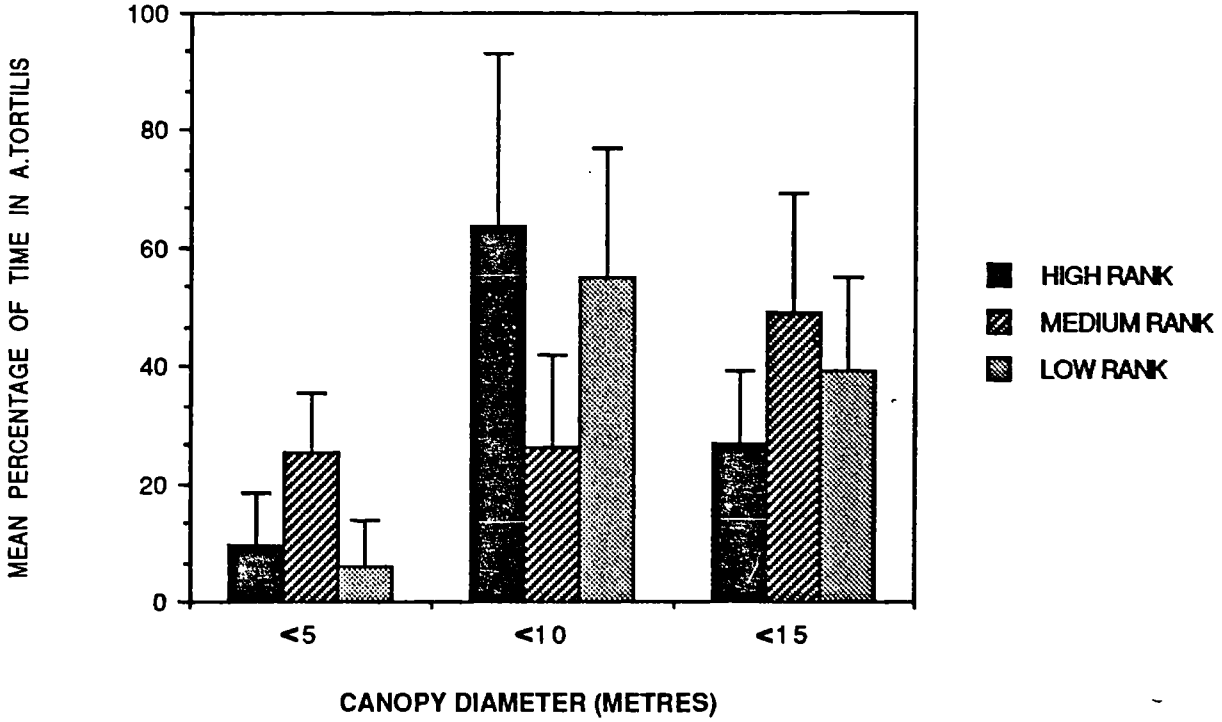


FIGURE 7.7: RELATIONSHIP BETWEEN RANK AND SIZE OF A. TORTILIS TREES OCCUPIED



plotted the relative frequencies of the different size categories for each species. Larger trees are evidently less common, yet they are clearly selected; this is shown by calculating selection ratios (percentage of feeding time allocated to each size category, divided by percentage abundance) for the two species; these are plotted in Figure 7.9. Larger trees may also be less defendable, and this could account for the smaller differences between rank categories at the largest size. For one species, then, but not for the other, HRFs may have monopolised the larger (hence richer) and rarer trees.

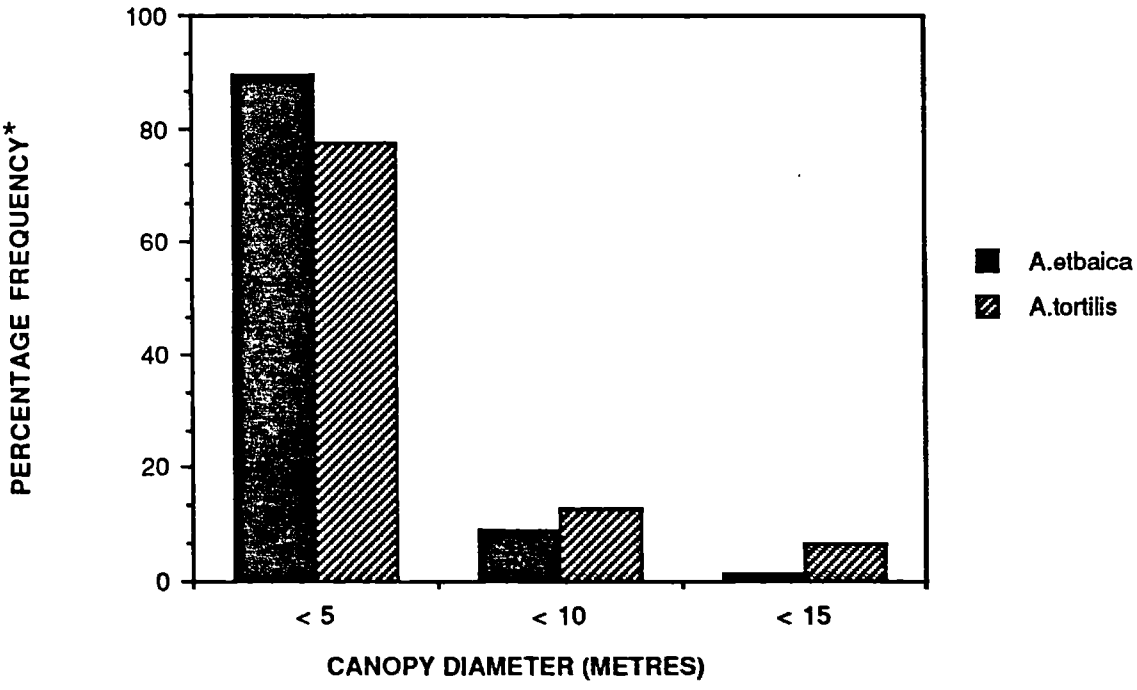
(c) Supplanting

Rates of feeding supplants were calculated for each of the focal adult females. Unlike in the provisioned group, rank was positively correlated with the rate at which supplants were given (r_s=0.659, df=16, p=0.002), but uncorrelated with the rate at which they were received (r_s=⁻0.248, df=16, p=0.320). The ratio of supplants given to supplants received was positively correlated with rank (r_s=0.699, df=16, p=0.001)

6. DISCUSSION

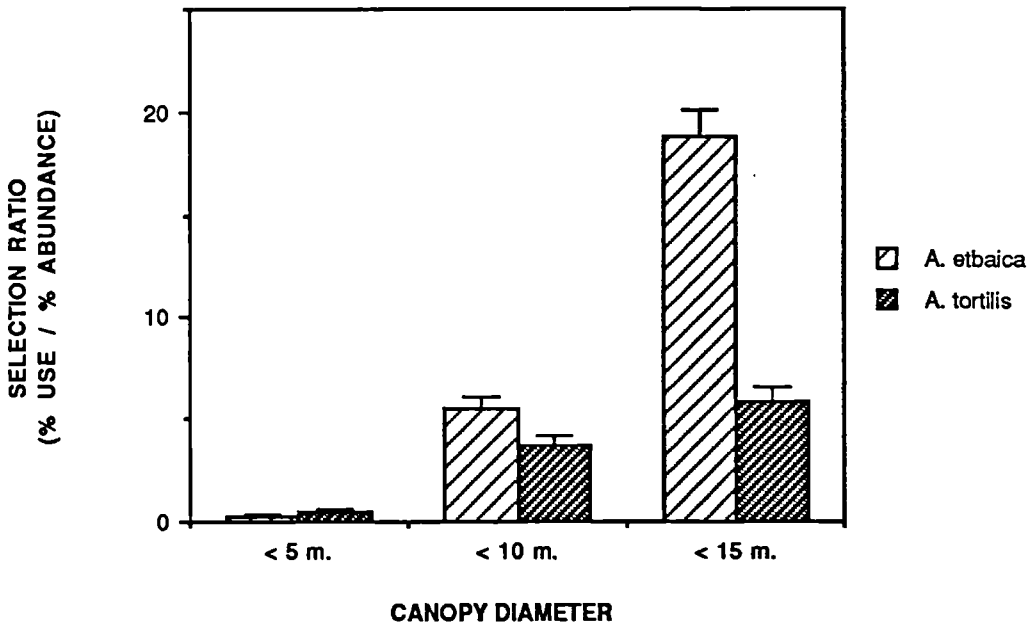
I have attempted to document some of the behavioral processes mediating the relationship between ecology and social organisation amongst females. Specifically, I have shown that the spatial locations of foraging individuals within the group were related to their dominance ranks, and that, under certain conditions of food distribution, high-rankers had priority of access to the best feeding sites. Competition was most

FIGURE 7.8: RELATIVE FREQUENCIES OF DIFFERENT SIZED ACACIAS



* Frequencies estimated from 30 m. quadrats.

FIGURE 7.9: SELECTION OF DIFFERENT SIZES OF ACACIAS



intense, and the influence of rank on ingestion rates was most apparent, for foods which occurred in high-density clumps. These were primarily foods eaten in the dry season.

a. Competition, resource charactersitics and seasonality

The patterns of competitive exclusion were extremely clear-cut in the provisioned group, for which food was supplied in a single, high-density "super-patch". Similar patterns were observed by Belzung and Anderson (1986) in an experimental study of feeding competition in rhesus macaques (*Macaca mulatta*); high-rankers ate first and ate most, whereas low-rankers tended to remain on the periphery and ate little. Other authors working on female cercopithecines have also noted an exacerbation of competition amongst provisioned animals (Sugiyama and Ohsawa, 1982, Fairbanks and McGuire, 1984; Altmann and Muruthi, 1988). Harcourt (1987) argues that "it is probably the distribution of food that is important, not its abundance". Thus the potential for despotism is, in theory, inversely related to the degree to which food is dispersed, irrespective of how much there is of it. Harcourt's argument is supported in the present case, since the highest levels of competition in the naturally-foraging group were evoked by foods occurring in high-density clumps. However, the idea that competition *tends* to be greatest during periods of relative scarcity (e.g. Post *et al.*, 1980; Gouzoules *et al.*, 1982) also received some support, probably because foods which were eaten in the dry season also happened to be relatively clumped in distribution.

I have stressed that inferences about seasonal patterns in the behavioural ecology of these baboons are subject to the qualification that a fairly limited period has been sampled (12 months for ranging, 10 months for feeding, and only 8 months for biomass estimates and detailed behavioural data on separate individuals). There is, however, evidence from other sources supporting the claim that, amongst baboons, competition tends to be most intense in the dry season. Post (1978) found, as I have done, that the rate of feeding supplants was significantly higher in the dry season than in the wet season, and also that monthly rates were inversely related to cumulative rainfall. Whitten's (1983) study suggests that the situation is the same in vervet monkeys (*Cercopithecus aethiops*); most rank-related dietary differences were found in the dry season (although this was not when supplant rates were highest). In the present case, a period of drought and drastically reduced food availability in the year following the study culminated in the group splitting, possibly as a result of exacerbated intra-group competition.

What are the implications of this tendency for competition to increase with declining food availability? An obvious one is that dominance rank may influence female fitness primarily through effects on survival, particularly infant survival, rather than through effects on fecundity. It is intended that long-term data from Chololo will eventually be used to test the hypothesis, but in the meantime, evidence bearing on it is available from other studies. Busse (1982) reported a correlation between female rank and infant survival in chacma

baboons (*P.ursinus*), and Bulger and Hamilton (1987) found that, at large group sizes, high-ranking females of the same species had significantly greater offspring survival than did low-rankers. Altmann *et al.* (1988) found that offspring survival to age 6 years among *P.cynocephalus* was an interactive function of offspring sex and female rank; the sons of high-rankers were more vulnerable than their daughters, whereas the reverse was found for low-rankers. High-rankers' daughters survived better than low-rankers' daughters, but high-rankers' sons survived less well than low-rankers' sons. The pattern of survivorship can be summarised as follows:

HRF daughters	>	LRF sons	>	LRF daughters	>	HRF sons
p=0.47		p=0.33		p=0.25		p=0.00
n=15		n=9		n=4		n=5

Where p is the probability of surviving to age 6, and n is the number of offspring in the sample.

In terms of actual *numbers*, this corresponds to 1 surviving offspring per female for HRFs and 0.57 for LRFs, but the parameter "surviving offspring" is obviously partly a function of the number of births. These data do not, therefore, give a clear indication as to whether there is a general relationship between rank and offspring survival, and, as Altmann *et al.* (*op. cit.*) stress, firm conclusions must await more data. What was clear from the available evidence, was that rank strongly influenced the age at which a female reproduced for the first time. This component of lifetime reproductive success is presumably a function of pre-pubertal growth rates, and so could equally be influenced by a young females' ability

to make the most of good conditions as by her ability to ameliorate the effects of periods of food scarcity.

Cheney *et al.* (1988) found no correlation between female rank and overall infant survivorship among vervet monkeys (*Cercopithecus aethiops*), but low-ranking females and their offspring were more likely than high-rankers to die during periods of food shortage. This did not translate into overall mortality differences because high-rankers were more susceptible to predation, the reason for which was unclear. There was no evidence that competition lowered the fecundity of low-ranking animals. In contrast, vervets studied by Whitten (1983) in a different area did show a positive association between rank and fecundity, high-rankers breeding earlier and having higher birth rates than low-rankers. Offspring survival was not significantly related to rank. In macaques (*Macaca*), however, associations between rank and mortality rates have been documented (*M.sinica*; Dittus, 1979: *M.fuscata*; Sugiyama and Ohsawa, 1982: *M.mulatta*; Drickamer, 1974; Wilson *et al.*, 1978: *M.fascicularis*; Silk *et al.*, 1981: *M.sylvanus*; Paul and Thommen, 1984: see also Harcourt, 1987).

To summarise, there is good evidence for an association between dominance rank and mortality in at least some populations of cercopithecine monkeys. Nevertheless, it is also the case that some populations exhibit a relationship between rank and fecundity (see Harcourt, 1987, 1989, for reviews).

Which component of female fitness is most affected by rank will presumably depend on ecological circumstances; where resources are most clumped during periods of scarcity, rank may affect survival more than it does fecundity. The situation is complicated, however, by the fact that infant mortality and interbirth interval (IBI) are related; IBIs are reduced where infant mortality is high, because females quickly become pregnant again when an infant dies (Harcourt, 1987, 1989). Thus, if the offspring of HRFs survive better than those of LRFs, any tendency for the former to be more fecund may be overidden. Conversely, where rank does not influence infant mortality, effects on fecundity may emerge. Clearly, further study is needed of the relationships between seasonal clumping of resources, feeding competition, and patterns of reproduction and mortality.

Like Shopland (1987) I was unable to demonstrate a relationship between food quality and rates of supplanting or spatial clustering. Shopland did, however, find that the probability of an attempted supplant being unsuccessful (p_u) was higher when the yield (amount harvested per unit time) was low; she interpreted this result as indicating that individuals were less willing to give up their position when feeding on items that were hard to process, because the cost in wasted time and energy was greater. If this is so, then it can be further predicted that p_u will be positively related to the elapsed time spent attempting to extract items (such as underground corms and roots) prior to the attempted interruption; this remains to be tested.

The present study and the one by Shopland (*op cit.*) produced contrasting results concerning the effect of resource clumping on the intensity of competition in baboons. Shopland found no difference between clumped and dispersed foods in either the associated supplant rate or the number of neighbours. Elsewhere, experiments on captive macaques (*Macaca mulatta*) have demonstrated that clumping of food results in high levels of aggression (Southwick, 1967; Belzung and Anderson, 1986; Boccia *et al.*, 1988). Monaghan and Metcalfe (1985) observed a similar phenomenon amongst wild brown hares (*Lepus europaeus*). During the provisioning experiment at Chololo, individuals in MLK group engaged in supplants at a rate of 1 every 2.5 minutes, which contrasts strongly with the mean of 1 every 29.9 minutes for the naturally-foraging group; the only natural food which evoked supplants at a rate approaching that seen during provisioning was *Cyperus blysmoides* corms (1 every 4.33 minutes). These were highly clumped in distribution (see Chapter 3), but they also took considerable time (and presumably energy) to dig up, and it is to this latter factor that Altmann (1980) attributed the high supplant rates evoked by corms at Amboseli, where they do not occur in clumps. Altmann's explanation, however, seems to conflict with the lack of any association between yield or processing value and supplant rate in Shopland's study.

It is to be expected that seasonal variability in levels of competition are mirrored by geographic variability, although one then has the additional factor of group size and demography to take into consideration. Unfortunately, differences between study sites in the reported rates of

supplants are probably not a very reliable indicator of variation in the level of competition. Even when very similar behavioural definitions are used, there are likely to be observer differences in sensitivity and attention to particular behaviours. In the present study, for example, the detailed recording of feeding must surely have compromised the detection of subtle interactions. This "observer effect" is suggested by comparing rates reported from a single study site, Amboseli (the species being *P.cynocephalus*), by different workers. Post (1978) recorded an average feeding supplant rate for adult females of 1 every 11.8 minutes (calculated from his Table 45), whereas Altmann (1980) observed a range of between about 1 every 17 minutes and 1 every 100 minutes, also amongst adult females (estimated from her Figure 27). Finally, Shopland recorded a mean of 1 every 6.9 minutes; this higher rate may be partly attributable to the fact that her subjects were juveniles, but also probably to the fact that feeding supplants were a major focus of her observations. Because of this inevitable variation, it is not possible to make direct comparisons with any confidence. Where differences are extreme, however, these may be taken as indicative of real population variability. Amongst mountain baboons (*P.ursinus*) studied in the Drakensberg region of South Africa, feeding supplants were observed at a rate of only 1 every 100 hours! (R. Byrne, pers. comm.); here group size was small, foods were mostly widely dispersed, and there were no predators forcing foraging groups to bunch together for protection. Intra-group competition in that case can therefore be presumed to have been minimal.

b. Spatial deployment, supplants, feeding, and predation

I have argued that dominance influenced foraging success through the medium of spatial deployment; high-rankers monopolised the richest feeding sites, and were thus able to achieve relatively high ingestion rates. Similar associations between rank and spatial positioning have been found in other work on baboons. Collins (1984), working on yellow baboons (*P.cynocephalus*) found that HRFs spent more time in clusters, whereas LRFs were more often in peripheral positions. Busse (1984) found that HRFs amongst chacma baboons (*P.ursinus*) had smaller "domains of danger" (the area containing all points nearer to the individual than to any other potential prey animal), and that, in one group, rank was positively correlated with the mean number of neighbours within 5 metres. More generally, much debate has surrounded the issue of whether baboon troops are coherently organised during group movements in such a way that the more vulnerable members are protected (e.g. DeVore and Washburn, 1963; Rowell, 1969; Rhine, 1975; Rhine *et al.*, 1979, 1980, 1981; Rhine and Westlund, 1981; Harding, 1977; Altmann, 1979).

Whereas these authors have mostly emphasised the anti-predator significance of spatial deployment, I, in common with a number of other authors, have been concerned with its relevance for feeding. Imanishi (1957) and Yamada (1966) reported that high-ranking individuals in groups of Japanese macaques (*Macaca fuscata*) tended to occupy the centre of the group, where they monopolised resources. In a study of baboons (*P.cynocephalus*), Collins (1984) suggested that the greater

propensity of HRFs than LRFs to be found in clusters might be the result of the latter suffering competitive exclusion. Robinson (1981) found that the dominant female and the dominant male in a group of capuchins (*Cebus nigrivittatus*) occupied the centre-front positions during foraging, and thus accrued significant foraging advantages. A relationship between spatial position and foraging success has also been documented for woodpigeons (*Columba palumbas*) foraging in flocks (Murton *et al.*, 1971), although in that example individuals near the front of the flock were at a *disadvantage*, due to continual displacement by the individuals behind. Finally, van Noordwijk and van Schaik (1987) studied groups of long-tailed macaques (*Macaca fascicularis*) which formed foraging sub-groups during the day. Here, low-ranking females were more prone than high-rankers to avoid direct competition, by splitting off from the main group into small foraging parties. When they did remain in the main group, they suffered a depression in the rate at which they harvested fruit.

The anti-predator and feeding implications of spatial positioning may, however, be interdependent. Hamilton (1971) argued that vulnerability to predators will, in general, be greatest for those individuals which are distant from neighbours and for those at the edge of the group. The tendencies of HRFs to be located in central positions, to be surrounded by less unoccupied space, and to feed more in trees, could reduce their susceptibility to predation. This, in turn, could reduce the amount of time needed for vigilance, and hence increase the harvesting rate. An inverse

relationship between vigilance time and harvesting rate has been demonstrated in several species of birds (e.g. Powell, 1974; Lazarus, 1979; Caraco *et al.*, 1980), as has a tendency for peripheral individuals to spend more time in vigilance (Horn, 1968; Jennings and Evans, 1980; Inglis and Lazarus, 1981).

The only published study of the interaction between spatial positioning, vigilance and foraging success in a primate is Robinson's (1981) study of capuchins. In these monkeys, as in birds, occupation of central positions was associated with less time spent in vigilance and greater foraging success. In their study of long-tailed macaques, Van Noordwijk and Van Schaik (1987) found that low-ranking females maintained their foraging success at a level comparable to that of high-rankers only by moving outside the main party, thereby increasing their vulnerability to predators. These authors also suggested that competition within baboon groups might be primarily for "safe positions", but neither the existence of such safe positions, nor a trade-off between vigilance and foraging, has been empirically demonstrated; for a genus whose adaptations are thought by many to have been extensively moulded by predation (e.g. Hall and DeVore, 1965; Crook and Gartlan, 1966; Altmann and Altmann, 1970; Dunbar, 1988), this is surely an omission.

Some authors have argued that supplants directly suppress the foraging success of subordinates (Slatkin and Hausfater, 1977; Post, 1978; Post *et al.*, 1980), while others have emphasised the importance of spatial deployment patterns that result from

subordinates avoiding direct competition with dominants (Robinson, 1981; Furuichi, 1983; Whitten, 1983; van Noordwijk and van Schaik, 1987). It should be noted that the first set of references given are all for the same species (*Papio cynocephalus*), and from the same study site at that. Thus the difference of emphasis may reflect genuine species- or population-differences. On the other hand, it could also reflect the simple fact that spatial deployment has been little studied at Amboseli.

Variation in predation pressure could perhaps result in variation in the degree to which individuals cluster together (van Schaik, 1989), hence influencing the rates of direct confrontation; where predators are scarce, low-rankers could spread out and find alternative feeding sites. The problem with this idea is that it implies that the vervets in Whitten's study were less vulnerable to predation than the (much larger) baboons at Amboseli, an unlikely possibility, and one for which there is no evidence.

Like Post (1978) and Altmann (1980), I found that supplant rates were related to dominance rank. It has not been possible here to specify what direct effects this had on foraging success. Although the rates were rather low (on average, about 1 every 30 minutes of feeding time), if they were used to gain initial access to rich food patches, they could still have had an important direct impact on spatial positioning and foraging success. Supplant rates were not clearly related to spatial position in the provisioned group once the group had settled at the food patch, but it was

argued that supplants could have served to establish those positions initially. Other authors have suggested that feeding supplants are often used as a form of "pure interference" (Shopland, 1987), to reinforce dominance relations even at some energetic *cost* to the supplanter (Johnson, in prep.). As yet we have no idea of the relative frequency of "genuine" feeding supplants and "social" feeding supplants.

CHAPTER 8: CONCLUDING DISCUSSION

Having already discussed each set of results in detail, I will confine myself here to the implications of two general themes which have been pervasive.

1. ECOLOGICAL CONTRASTS BETWEEN MALES AND FEMALES

It has long been appreciated that unequal material contributions by males and females to the production of offspring will theoretically lead to the evolution of morphological, physiological and behavioural differences associated with the divergent reproductive strategies of the two sexes (Bateman, 1948; Trivers, 1972; Wade, 1979). Amongst mammals, females make a far greater material contribution than do males. Hence females' reproductive success should be primarily limited by their ability to channel resources into rearing offspring, while males will be primarily limited by the number of females to which sexual access can be gained.

These conclusions have a number of implications, two of which are considered here. Firstly, the divergent selection pressures associated with reproduction in females and males are thought to underlie the evolution of sexual dimorphism in body size (e.g. Clutton-Brock, 1985). The primary emphasis of discussion, however, has been on only one half of the story; the effects of sexual selection on male size (e.g. Darwin, 1871; Clutton-Brock *et al.*, 1977; Clutton-Brock, 1985;

Alexander, 1979; but see Ralls, 1977). Progress in understanding the evolution of dimorphism therefore demands consideration of the likely role of reproductive selection pressures in determining female size. It has also been argued that, whatever the precise explanations for the phenomenon, body size dimorphism may have secondary influences on behavioural ecology (Clutton-Brock, 1977), and primatologists have been particularly interested in sex differences in dietary composition. In sum, we can expect dimorphism to have important ecological implications. Secondly, we might expect female behavioural strategies to reflect the paramount importance of nutrient-acquisition, while males may compromise foraging efficiency by investing time and energy in gaining and maintaining access to fertile females; while generally valid, this kind of thinking may have led to an underestimation of the importance of nutrition in males. The two issues are addressed separately below.

(a) Ecological implications of sexual dimorphism

Baboons are strongly dimorphic in body size (Dunbar, in press). Nevertheless, in the present study, lactating females had daily food intakes very similar to those of males, suggesting that male and female body sizes are limited by common ecological-energetic constraints, with the addition of reproductive costs in females. The idea that sexual dimorphism in animals may in part reflect energetic strategies by reproducing females has been discussed before (Jones, 1973; Wiley, 1974; Downhower, 1976; Ralls, 1977; Demment, 1983; Price, 1984; Saether and Haagenrud, 1985). Price (1984) for example, suggests that both males and females may be held off

the survival optima for body size, the former by sexual selection (usually for larger size), the latter by fertility selection (usually for smaller size). He argues that evaluation of mortality rates can reveal which sex is closer to the survival optimum. In a population of Darwin's finches (*Geospiza fortis*), Price (op. cit.) found a fertility advantage accruing to small females, but a survival advantage to large individuals (hence to males) during a drought. The degree of dimorphism within mated pairs bore no relationship to reproductive success, arguing against the niche separation hypothesis for the evolution of size differences.

Dimorphism in baboons may be related to mortality and fertility in similar ways. The ability to survive periods of food shortage (fasting endurance) is theoretically a positive function of body size in mammals, because metabolic rate increases with body size more slowly than do fat reserves (Lindstedt and Boyce, 1985). This is likely to have important demographic consequences for baboons, because of the marked seasonality and occurrence of energy bottlenecks in savannah environments (see Chapter 3). Indeed, higher mortality in females than in males during food shortages has been reported for baboons (Hamilton, 1985; Altmann *et al.*, 1988). However, the picture is complicated by the fact that females' smaller size means they are also subordinate to males; hence, differences in survivorship through seasonal bottlenecks may be related to inter-sexual competition (Hamilton, 1985), as well as to energetic implications of size. A further complication in evaluating the implications of dimorphism for sex-specific mortality rates in matrilocal populations is that

males are exposed to additional risks during migration between groups (Dunbar, 1988). At present, therefore, it is not possible to draw firm conclusions concerning the nature and causes of sex differences in mortality.

Variation among baboon populations in body weight and dimorphism has been examined by Popp (1983), and, with a more extensive data set, by Dunbar (in press). Both authors found a relationship between mean annual rainfall and male weight. Dunbar also found a relationship between female weight and rainfall, but the correlation was weaker than in the case of male weight. Conversely, ambient temperature was found to be a stronger influence on female weight than it was for male weight. Overall, however, female weight showed less variance across populations than male weight did. Dunbar suggested that these differences reflect differences in reproductive strategies, arguing that, while large size is crucially important for males, resulting in a delay in the onset of breeding, females should start to reproduce as early as possible. Hence males may take advantage of better quality habitats by growing larger, while females take advantage by reaching menarche earlier. The stronger influence of temperature on females was explained by the fact that, since males are larger anyway, they will be less prone to variation in thermoregulatory energy costs; this makes sense because the crucial factor is probably the amount of time at night spent below the lower critical temperature (see Chapter 6).

These arguments lead to the suggestion that female size represents a compromise between selection for low basal energy

requirements during reproduction (hence small body size), and selection for factors such as temperature tolerance, digestive capability (see Demment, 1983) and fasting endurance (hence large size). Large size in males may be promoted by sexual selection acting on competitive ability, and/or the same factors promoting large size in females; the problem is then to determine what constrains males from growing even larger. One answer, suggested by Demment (1983), is that male size is limited at the upper end by competition with ruminants, which are more efficient at digesting the fibrous foods that would have to be incorporated into the diet to satisfy increased energy requirements. The situation in baboons appears to differ from that in populations of the Norwegian moose (*Alces alces*), where the onset of reproduction is apparently determined by age rather than by size, female weight varies more than male weight does, and dimorphism is more closely correlated with variation in female weight than it is with variation in male weight (Saether and Haagenrud, 1985).

Dietary sex differences have been interpreted both as a *function* of dimorphism, in the sense that dimorphism has evolved under selection for niche separation, and as a *secondary consequence* of it (Selander, 1966; Clutton-Brock, 1977; Post, 1978; Price, 1985). For example, in reviewing field studies of primates, Clutton-Brock (1977) suggested that sex differences might be a result of body size constraints, the physiological impact of reproduction on females, or the need to avoid excluding mates from valuable resources. A fourth possibility, alternative to the third, is that sex differences directly reflect competitive exclusion of the less

powerful sex. In general, inter-individual variance in diet in the present study, at the level of gross nutrient composition, was surprisingly low. This conflicts with a reasonable body of data in the literature on primates which suggests both that competition leads to rank-related differences in diet quality (e.g. Dittus, 1979; Wrangham and Waterman, 1981; Whitten, 1983) and that males and females eat different diets (Clutton-Brock, 1977; Post, 1978; Demment, 1983).

In fact, the evidence supporting claims for dietary sex differences is generally rather flimsy, because it is often the case that too few individuals (particularly males) are sampled to allow generalisations to be made with confidence. For example, in three out of the four published studies cited by Clutton-Brock (1977) as demonstrating sex differences in plant feeding, only two males were sampled (Pollock, 1977; Rodman, 1977; Fossey and Harcourt, 1977); in the fourth study, three males were sampled (Waser, 1977). Post's use of two males and two females in his study of baboons (*P.cynocephalus*) was mentioned in Chapter 5, and these sample sizes also apply to Demment's (1983) calculations, since he used Post's data. Studies by Harrison (1983) on green monkeys (*Cercopithecus sabaeus*) and by Watts (1984) on gorillas (*Gorilla g. berengei*) involved larger samples, and so provide stronger claims for real sex differences. However, it is not yet possible to discern any general trends in terms of what types of food or nutrient are implicated. Further extensive study would be required to establish whether marked sex differences are the norm, in which species and under what

conditions they are most likely to occur, and, where they do occur, what their nature and functional significance is.

In the present case, in which seven males and nineteen females were sampled, no strong differences in either diversity or nutritional composition of the diet were found, despite a tendency of females to spend more time foraging in trees. This lack of dietary sex differences coupled with the failure to demonstrate clear trends within the primates generally, suggests that the idea of niche separation may have been overemphasized. A question that remains for future analysis is whether the composition of diets nevertheless differed in terms of plant species and parts; if so, this would suggest that males and females were able to arrive at similar nutritional endpoints via different dietary routes. It is possible, for example, that females were forced by competition with males to utilise items which were harder to find and/or process, but which were phytochemically similar. The fact that sex differences in total nutrient intake and in time spent feeding correspond quite closely (Chapter 6) does, however, argue against this suggestion.

(b) Implications of foraging and nutrition in males

In the present study, the importance of nutrient-acquisition for females was indicated by the occurrence of tangible competition. I did not, however, evaluate whether this was also true of males, and research on feeding competition elsewhere has also tended to focus on females (e.g. Wrangham,

1980, 1983; Whitten, 1983, 1988; van Noordwijk and van Schaik, 1987; Harcourt, 1989: but see also Dittus, 1979; Post *et al.*, 1980).

The idea that, amongst males, foraging strategies are less important than mate-acquisition strategies (e.g Wrangham, 1980) is, however, perhaps a little too simplistic. The reason for this is that the outcome of reproductive competition between males may itself be influenced by nutrition. Firstly, gaining and maintaining access to fertile females in multimale baboon troops can be extremely energetically expensive (Hausfater, 1975; Bercovitch, 1984; Smuts, 1985; Strum, 1987; pers. obs.), and an undernourished or otherwise weak male would no doubt be at a considerable disadvantage. Secondly, sperm competition is thought to be intense amongst male primates living in multimale groups, since females frequently consort with several males sequentially during oestrous (Smuts, 1985; Strum, 1987; pers obs.), and males show morphological adaptations for producing large amounts of sperm (Short, 1981; Harcourt *et al.*, 1981; Harvey and May, 1989); anything which affects the quantity or motility of sperm is therefore likely to affect insemination success. Little has been published on the relationship between nutrition and sperm production, but amongst domestic cattle sperm counts are positively correlated with caloric intake (Moustegaard, 1977). These considerations suggest that the influence of foraging strategies and nutrition on reproductive success amongst male baboons deserves examination, and that it may not make sense to speak

of fertile females as being "uniquely valuable" resources (Wrangham, 1980).

2. FEEDING COMPETITION, PREDATION AND SOCIAL EVOLUTION

At the beginning of this thesis I commented on the recent valuable rapprochement between the two previously rather disparate areas of primate behavioural ecology and socioecology on the one hand, and the study of social relationships on the other. It is thus, I suggested, that our understanding of the processes of social evolution can be advanced. I will now try to link the work that I have presented here with attempts to produce comprehensive ecological models of primate social organisation and relationships.

Relationships between individuals are the building blocks of societies (Hinde, 1976b, Dunbar, 1989), and it is the recognition of this that has guided much recent work in primate socioecology. The most influential attempt, at least until recently, to explain variation in social relationships has been Wrangham's (1980) model of female-bonded groups, which was predicated on certain patterns of feeding competition (see also Chapter 1). How do savannah baboons fit in with the ecological conditions specified by Wrangham?

Wrangham (1980) envisaged the diets of female-bonded primate groups as consisting of two components, the "growth" diet,

eaten during periods of abundance, when populations are expanding, and the "subsistence" diet, eaten during periods of scarcity, when populations are declining. Subsistence diets, Wrangham argued, should consist of low-quality food found in large, uniform patches, allowing group members to coexist with minimal competition when food is scarce. Then, when rich patches of high-quality food become available, these can be exploited by the whole group, insofar as it is able to exclude neighbouring groups. It is these "rich pickings" that, in Wrangham's model, provide the *raison d'etre* for female-bonded groups.

The conditions specified in Wrangham's model do not appear to be met amongst baboons, because, as noted, competition *increases* during the dry season. Wrangham correctly noted that savannah-dwelling populations do not rely extensively on fleshy fruits, and that the seeds, pods and flowers which are utilised "tend to be available for short periods at restricted locations, where aggressive competition occurs for access to feeding sites" (Wrangham, 1980). What may be incorrect about this part of Wrangham's argument is the contention that such foods make up the so-called growth diet; as we have seen (Chapter 5), in the present study they were available and eaten principally in the dry season. During the period of abundance (the wet season), much of the diet was made up of grass blades and other foliage, as in Post's study (1978), and these foods are relatively homogenous in their disribution. Wrangham (p.274), however, assumed that they represent subsistence foods.

The implication of this reversal of the conditions specified by Wrangham is that the functional significance of group living in these baboons is either related to survival through seasonal bottlenecks, rather than to exploiting growth foods when conditions are good, or to some factor other than feeding competition, such as predation (c.f. van Schaik, 1983, 1989; Dunbar, 1988). It is important, as Janson and van Schaik (1988) have emphasised, to maintain a clear distinction between intra- and inter-group competition. Since I have not measured the latter, I cannot be sure that the two processes display similar seasonal trends (or even that inter-group competition was significant). Thus, theoretically, it is still possible that *groups* competed with each other more in the wet season. In fact little is known about inter-group competition in primates (see Janson and van Schaik, 1988; van Schaik, 1989), let alone in baboons, and this will be an important area for future investigations aiming to test functional hypotheses about social organisation.

Recently, the topic of ecological influences on social relationships in female primates has been reassessed by van Schaik (1989), who, contrary to Wrangham, emphasizes the likely role played by predation. Van Schaik begins with the proposition that there are essentially three types of competition affecting female relationships; scramble competition within groups, contest competition within groups, and contest competition between groups (see also Introduction to Chapter 7). In gregarious species or populations, strong inter-group contest competition should result in egalitarian hierarchies, rather than the despotic variety observed, for

example, amongst baboons and macaques. This is because subordinate females would be expected to leave the group, thereby reducing its ability to compete with other groups, wherever the subordinates suffered excessively from contest competition with dominants. Thus, under these conditions, dominants should refrain from exerting their full power.

Van Schaik contrasts this situation with the one in which there is little inter-group contest competition and marked intra-group contest competition. Intra-group competition is expected where high predator pressure forces groups to be cohesive. Where intra-group competition is of the scramble variety - because food is either dispersed or occurs in patches large enough to feed the whole group - aggression over food will be ineffectual in enhancing individuals' intakes, and dominance hierarchies will be generally weak and egalitarian. It is therefore suggested by van Schaik that despotic, linear hierarchies reflect strong intra-group contest competition, and relatively weak inter-group contest competition. This pattern could, however, result from intra-group contest for positions with low predation risk, rather than from contest for food, if food is dispersed. Earlier, van Noordwijk and van Schaik (1987) argued that "The vervets, living in cohesive groups, competed mainly for food and perhaps also for safe positions, whereas in the baboons, feeding on dispersed foods, competition is more likely to be for safe central positions". Janson and van Schaik (1988) stated that no intra-group contest competition for food is discernible in baboons. Given the results of the present

study, in which females' dominance ranks strongly influenced their foraging success, this position should now be modified.

As noted in the previous chapter, competition for safe positions and competition for food may be interdependent. Thus, in the long-tailed macaques (*Macaca fascicularis*) studied by van Noordwijk and van Schaik (1987), competition for clumped food within the main party forced subordinates to forage in smaller sub-groups, in which predation rates were higher. This led the authors to conclude that "safety monopolization was the predominant mode of competition". In fact we may differentiate two types of "safety competition". Firstly, there is *pure* safety competition, unrelated to feeding; an example of this would be monopolisation of central positions in baboon groups during movements across open ground, or when feeding on dispersed food. Secondly, there is *indirect* safety competition, which is essentially competition for feeding sites resulting in peripheralisation, and hence increased vulnerability, of subordinates. Note that where pure safety competition occurs, this may still have the effect of lowering feeding rates in subordinates, by increasing their need for vigilance. Under such conditions as these, then, subordinates are subject to two conflicting forces; feeding competition from within the group tends to push them out to the margins, while predation risk has the opposite effect. It is the balance of these two forces which will determine the cohesiveness of the group. Where the risk of predation is low *relative to the costs of feeding competition* (but not necessarily low in absolute terms), groups will be less cohesive and may fission into separate

foraging parties at times when feeding competition is particularly intense, enabling low-rankers to forage relatively undisturbed (e.g. van Noordwijk and van Schaik, 1987). We can expect that the major costs of competition for subordinates in these circumstances will be increased foraging effort (time and/or energy expended), which is just what van Noordwijk and Van Schaik (*op. cit.*) found. Conversely, where predation risk is high relative to the costs of feeding competition, individuals should endure the depression in feeding rates engendered by remaining close to other troop members; the costs which result here will be primarily reduced food intake, as opposed to increased foraging effort. It is this latter scenario which seems to best fit Chololo baboons; its general applicability to savannah baboons would be most effectively addressed by comparative studies assessing inter-population covariation in predation pressure, group cohesion and the impact of competition on individuals' foraging profiles.

The fact that, in the present study, correlations were found between rank and the number of neighbours while feeding on clumped foods, but not while moving or performing other activities, suggests that competition was primarily for food, and that monopolisation of safe positions, if it occurred at all, was therefore indirect. Given the crudeness with which number of neighbours measures spatial deployment, however, further detailed study would be required to confirm this. Rather damaging for any safety competition hypothesis, however, is the finding that predation of vervet monkeys (*Cercopithecus aethiops*) at Amboseli was concentrated amongst

high-ranking rather than low-ranking females (Cheney *et al.*, 1988).

A final point concerns a limitation of this study. I am aware that, in focussing on the ecological implications of dominance rank amongst adult females, I have merely scratched the surface of baboon social complexity (see for example Strum, 1982, 1988; de Waal, 1986). Dominance amongst females is, after all, only one dimension of one type of relationship, and there is more to social organisation than simply resource competition among females. As van Schaik has warned, to try to account for variability in relationships *purely* in terms of ecology is to oversimplify, since "interactions between male and female strategies may result in different female relationships from those found in the absence of any male influence" (van Schaik, 1989, p.196). Smuts (1983, 1985), for example, has begun exploration of the functional implications of the "special relationships" (Strum, 1975) between males and females, which are commonly observed amongst baboons, speculating that individual females may benefit from such associations by an amelioration of intra-sexual competition, while males benefit by reproductive cooperation. Females appear to compete for access to particular males (Dunbar and Sharman, 1983; Smuts, 1985; Strum, pers. comm.). The precise costs and benefits of such relationships, however, have yet to be quantified.

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APPENDIX I: SPECIES LIST OF MAMMALS SIGHTED

Chiroptera
- Yellow-winged bat (*Lavia frons*)
- Spp. (*Pipistrellus*?)

Rodentia
- Crested porcupine (*Hystrix* spp.)
- Pallid ground squirrel (*Xerus rutilus*)
- Mouse spp. (*Murinae*)

Lagomorpha
- Cape hare (*Lepus capensis*)

Primates
- Lesser bushbaby (*Galago senegalensis*)
- Vervet monkey (*Cercopithecus aethiops*)
- Olive baboon (*Papio cynocephalus*)

Carnivora
- Dwarf mongoose (*Helogale parvula*)
- White-tailed mongoose (*Ichneumia albicauda*)
- Slender mongoose (*Herpestes sanguineus*)
- Common genet (*Genetta genetta*)
- Black-backed jackal (*Canis mesomalis*)
- Bat-eared fox (*Otocyon megalotis*)
- Wild dog (*Lycaon pictus*)*
- Aardwolf (*Proteles cristatus*)
- Spotted hyaena (*Crocuta crocuta*)
- Cheetah (*Acinonyx jubatus*)
- Leopard (*Panthera pardus*)
- Lion (*Panthera leo*)

Proboscidea
- Elephant (*Loxodonta africana*)*

Artiodactyla
- Kirk's dik-dik (*Rhynchotragus kirki*)
- Grimm's duiker (*Sylvicapra grimmia*)
- Oribi (*Ourebi ourebi*)
- Steenbok (*Raphicerus campestris*)
- Klipspringer (*Oreotragus oreotragus*)
- Gerenuk (*Litocranius walleri*)
- Kongoni (*Alcelaphus busephalus*)
- Beisa oryx (*Oryx beisa*)
- Cape eland (*Taurotragus oryx*)
- Impala (*Aepyceros melampus*)
- Thomson's gazelle (*Gazella thomsoni*)
- Grant's gazelle (*Gazella granti*)
- Buffalo (*Syncerus caffer*)
- Reticulated giraffe (*Giraffa camelopardalis*)
- Warthog (*Phacochoerus aethiopicus*)

Perissodactyla
- Grevy's zebra (*Equus grevyi*)
- Burchell's zebra (*Equus burchelli*)

* Transient

APPENDIX II: LIST OF FOODS

Grasses and Sedges	Parts eaten
Chloris roxburghiana	Blade bases
Cynodon dactylon	Blades, meristems
Cynodon plectostachyus	Blades, meristems
Cyperus blysmoides	Blades, corms
Cyperus merkeri	Swollen leaf bases
Cyperus obtusiflorus	Swollen leaf bases
Cyperus spp.	Swollen leaf bases
Dactyloctenium aegyptium	Flower
Kyllinga alata	Flower
Kyllinga alba	Flower
Kyllinga nervosa	Swollen leaf bases
Mariscus amauropus	Swollen leaf bases
Panicum maximum	Blades (distal portion)
Penissetum mezianum	Blades
Penissetum spp.	Blades
Sporobolus spp.	Seed heads
Tragus bertorianus	Flowers

Herbs	
Amaranthus graezicans	Leaves
Ammocharis tinneana	Leaves
Becium spp.	Inflorescences
Cissus rotundifolia	Dried leaves
Coccinea gradis	Leaves and stems
Commeline erecta	Floral buds
Commelina reptans	Stem bases, roots
Commelina spp.	Leaves
Commicarpus helenae	Fruits
Conostomium quadrangulare	Inflorescences
Farsetia steroptera	Inflorescences
Ipomoea kituensis	Flowers
Ipomoea mombassana	Flowers, fruits
Ipomoea wightii	Flowers
Ipomoea obscura	Flowers, fruits
Jasminum fluminense	Leaves
Lantana viburnoides	Fruits
Monsonia angustifolia	Roots
Notonia picticaulus	Leaves
Ocimum suave	Leaves+stems
Osteospermum vaillantii	Fruits
Oxygonum sinuatum	Leaves
Pelargonium quinguelobatum	Roots
Polichia campestris	Fruits
Trachyandra saltii	Leaves
Tribulus terrestris	Leaves, flowers, fruits
Spp.	Bulb
Spp.	Pods

Appendix II cont.

Shrubs

Asparagus africanus	Leaflets
Grewia tembensis	Fruits, flowers
Hibiscus flavifolius	Fruits
Hibiscus spp.	Fruits
Hibiscus spp.	Flowers
Lycium europaeum	Leaves
Sansevieria intermedia	Swollen bases, fruits
Sansevieria spp.	Roots
Solanum incanum	Unripe fruits
Solanum nigrum	Fruits
Solanum spp.	Fruits

Acacias

Acacia brevispicata	Leaflets, whole pods
Acacia etbaica	Flowers, soft green thorns, (whole pods)
Acacia drepanalobium	(Ant galls)
Acacia mellifera	Young leaves, flowers, whole *pods*
Acacia nilotica	Green seed kernels, dried *seeds*
Acacia tortilis	Flowers, green seed kernels, dried seeds
Acacia seyal	Flowers, green seed kernels, exudate
Acacia xanthophloea	Flowers, green seed kernels

Other trees

Canthium phyllanthoideum	Fruits
Commiphera coricea	Young leaves
Ficus ingens	Fruits
Rhus natalensis	Fruits

Succulents

Aloe spp.	Floral stems
Euphorbia gossypina	Stem tips
Euphorbia nyikae	Fleshy stem segments
Euphorbia spp.(*heterechroma*?)	Fleshy stems
Euphorbia spp.	Whole young plant
Opuntia vulgaris	Fleshy pads

Animal matter

Caterpillar	Whole
Coccoon spp.	Contents
Francolin	Eggs, adult
White-bellied bustard	Eggs
Passerine spp.	Eggs
Passerine spp.	Adult

Appendix II cont.

Animal matter

Grasshopper	Whole
Cape hare (*Lepus capensis*)	Whole, except fur
Dik-dik (*Rhynchotragus kirki*)	Whole, except fur
Gazelle (*Gazella granti*)	Whole juvenile, except fur
Scorpion spp.	Whole, except sting
Snail	Whole

APPENDIX III: PROXIMATE COMPOSITION OF CHOLOLO PLANTS

a. Water, protein, fibre and lipid.

	% WATER	% DRY WEIGHT PROTEIN	FIBRE	LIPID
1.GRASSES AND SEDGES				
Cynodon dactylon green blades	76.1	19.1	28.3	5.0
C.plectostachyus young green blades	74.3	36.0	18.7	11.0
" green blades	84.8	22.5	21.1	8.0
" stolon node meristem	80.0	30.4	17.6	9.0
Cyperus blysmoides green blades	81.7	15.5	26.7	9.0
" " " "	84.0	15.4	24.2	8.0
" " corms (+husks)	--	--	13.3	--
" " " (-husks)	39.0	5.8	1.3	3.0
C.merkeri swollen leaf bases	85.9	8.6	14.7	7.0
Kyllinga alba flowers	75.0	10.1	23.9	--
Mariscus amauropus swollen leaf bases	78.6	7.6	16.1	3.0
" " " " "	80.0	8.7	20.2	--
" " " " "	75.9	12.5	19.1	--
Penissetum spp. green blades	74.2	26.5	26.9	8.0
" " " "	83.1	31.6	27.3	7.0
Sporobolus spp. seed heads	62.5	13.2	37.6	--
Tragus bertorianus flowers	76.3	14.6	25.5	--
2.HERBS				
Amaranthus graezicans leaves	85.6	31.9	12.3	--
Ammocharis tinneana leaves	87.3	30.9	12.7	--
Becium spp. infl.	81.9	19.5	18.9	--
Commelina erecta floral buds	90.0	--	26.5	--
Commicarpus helenae fruits	61.6	20.8	24.8	--
Conostomium quadrangualare infl.	90.0	14.6	15.9	--
Ipomoea mombassana flowers	87.5	15.6	17.3	7.0
" " "	87.9	15.7	14.5	14.0
" " fruits (+hull)	72.5	18.8	26.9	--
" " " "	--	19.0	28.9	--
" " " (-hull)	--	24.8	19.9	--
I. obscura fruits (+hull)	77.8	18.1	19.9	--
" " " (-hull)	--	21.0	16.1	--
" " " (hull only)	--	13.8	38.3	--
I. spp. flowers	88.3	15.8	11.8	12.0
Neonotonia wightii leaves	69.0	19.9	28.5	--
Monsonia angustifolia roots	66.7	6.6	25.3	6.0
" " "	75.0	5.1	35.6	--
Osteospermum vaillantii fruits(+bract)	78.8	11.6	38.6	--
" " " (-bract)	71.1	12.3	48.5	9.0
Oxygonum sinuatum leaves	86.3	20.3	10.4	--
Pelargonium quinguelobatum root	72.0	--	23.1	--
Polichia campestris fruits	66.1	11.3	12.2	--
Trachyandra saltii leaves	94.0	26.4	20.4	--
" " "	92.5	24.8	16.9	--
" " "	91.0	30.4	19.9	--
" " infl.	89.3	28.2	16.3	--
Tribulus terrestris leaves	83.2	35.1	17.3	--
" " soft green fruits	82.2	18.2	29.1	3.0
" " green fruits	82.5	15.6	55.6	--
Spp. bulb	84.9	18.3	12.7	6.0

APPENDIX IIIa, cont.

3.SHRUBS				
Aloe spp. flower stem	90.6	8.4	24.7	--
Asparagus africanus leaflets	78.6	30.8	13.5	--
" " "	81.5	--	12.7	--
Grewia tembensis green fruits	85.0	12.7	46.8	--
Hibiscus flavifolius fruits	70.6	15.1	36.5	--
H. spp. fruits	58.3	--	32.5	--
Lycium europaeum leaves	82.6	37.7	12.2	--
" " "	87.9	34.9	16.1	--
Sanasavieria intermedia swollen bases	93.2	15.8	16.9	8.0
" " fruits	--	10.1	13.3	--
Solanum incanum green fruits	84.3	12.9	23.0	6.0
" " " "	80.9	12.2	24.3	5.0
" " ripe fruits	--	12.5	26.3	7.0
S. spp. unripe fruits	75.0	12.9	34.3	--
Spp. leaves	93.3	17.6	7.1	--
4.ACACIAS				
Acacia brevispicata leaflets	75.0	42.8	10.2	8.0
" " young pods	60.3	20.9	23.9	4.0
A.etbaica young pods	67.4	17.3	31.2	5.0
" " "	--	19.5	25.7	4.0
" mature pods	65.5	15.2	36.4	4.0
" " "	75.7	18.0	23.0	6.0
" flowers (+pedicel)	68.9	19.1	11.3	9.0
" flowers (-pedicel)	65.2	18.7	10.9	9.0
" flowers (-pedicel)	--	18.7	9.5	10.0
" soft green thorns	78.1	26.2	15.1	--
A.mellifera young pods	79.5	33.8	21.5	4.0
" " "	79.2	29.6	26.5	3.0
" " "	79.4	27.0	24.0	3.0
" mature pods	82.6	21.1	31.8	2.0
" " "	--	27.0	20.6	3.0
" dry seeds	18.2	39.9	16.9	12.0
" " "	6.7	34.9	16.9	13.0
" flowers (-pedicel)	76.4	34.6	9.6	8.0
" dry flowers (-pedicel)	36.4	22.8	15.1	8.0
A.nilotica pods (-seeds)	--	11.6	11.5	12.0
" fresh seed kernels	76.7	47.0	2.5	11.0
" " " "	72.3	--	3.6	12.0
" fresh seed skins	50.0	12.0	21.4	4.0
" " " "	67.0	12.0	22.1	4.0
" flowers (+pedicel)	60.5	12.8	12.2	3.6
A.tortilis pods (-seeds)	61.0	10.8	29.6	3.0
" fresh seeds (+skins)	63.2	27.9	17.7	3.0
" flowers (+pedicel)	73.5	19.1	16.7	7.0
A.seyal pods (-seeds)	68.2	14.4	37.9	5.0
" fresh seeds (+skins)	71.1	29.4	12.9	4.0
" fresh seed kernels	74.4	48.3	3.4	8.0
" " " "	73.6	50.0	5.1	7.0
" fresh seed skins	66.7	15.1	22.7	3.0

APPENDIX IIIa, cont.

5.OTHER TREES				
Canthium phyllanthoidium fruits	67.1	7.2	22.8	--
Commiphora coricea leaves	77.8	27.1	10.4	--
6.EUPHORBIAS				
Euphorbia nyikae fleshy stems	89.1	7.6	26.1	8.0
E. spp. (heterochroma?) stems	90.8	10.8	17.3	10.0
" " "	88.9	13.7	15.3	--
7.MISCELLANEOUS				
Mushrooms spp.	66.7	9.2	--	--
Caterpillars spp.	85.7	--	--	--

b. Secondary compounds

	% dry weight TOTAL PHENOLICS	CONDENSED TANNINS	ALKALOIDS
1.GRASSES			
Cynodon dactylon green blades	1.3	0.0	0
C.plectostachyus young green blades	1.6	0.0	0
" green blades	1.3	0.0	-
" stolon node meristem	1.2	0.0	-
Cyperus blysmoides green blades	1.4	2.3	-
" " " "	1.6	2.8	-
" " corms (+husks)	0.8	1.8	0
" " " (-husks)	0.4	0.9	-
C.merkeri swollen leaf bases	0.9	7.3	0
Kyllinga alba flowers	1.1	0.0	0
Mariscus amauropus swollen leaf bases	1.0	3.1	0
" " " " "	0.9	5.6	-
" " " " "	1.0	7.9	-
Penissetum spp. green blades	1.3	0.0	-
" " " "	1.5	0.0	-
Sporobolus spp. seed heads	2.4	2.4	0
Tragus bertorianus flowers	0.8	0.0	-
2.HERBS			
Amaranthus graezicans leaves	1.6	0.7	0
Ammocharis tinneana leaves	4.2	3.4	+++
Becium spp. infl.	7.6	5.6	0
Commelina erecta floral buds	--	--	0
Commicarpus helenae fruits	1.5	0.0	0
Conostomium quadrangualare infl.	1.8	0.0	0
Ipomoea mombassana flowers	1.6	0.6	-
" " "	1.6	0.8	-
" " fruits (+hull)	0.8	0.0	-
" " " "	1.0	0.0	-
" " " (-hull)	0.8	0.0	0
I. obscura fruits (+hull)	0.7	0.0	-
" " " (-hull)	0.9	0.0	0
" " " (hull only)	1.0	0.0	-
I. spp. flowers	0.7	0.7	-

APPENDIX IIIb, cont.

Neonotonia wightii leaves	1.5	0.7	0
Monsonia angustifolia roots	8.1	1.1	0
" " "	6.6	1.4	-
Osteospermum vaillantii fruits(+bract)	0.6	0.0	-
" " " (-bract)	0.5	0.0	-
Oxygonum sinuatum leaves	3.9	2.0	-
Pelargonium quinguelobatum root	8.5	4.1	0
Polichia campestris fruits	2.6	0.0	0
Trachyandra saltii leaves	1.7	0.0	-
" " "	1.9	0.0	-
" " "	1.3	0.0	-
" " infl.	3.6	0.0	-
Tribulus terrestris leaves	1.4	0.0	0
" " soft green fruits	0.5	0.0	0
" " green fruits	0.4	0.0	-
Spp. bulb	2.9	0.0	0

3.SHRUBS

Aloe spp. flower stem	0.8	0.0	0
Asparagus africanus leaflets	3.8	0.0	0
" " "	5.3	0.0	-
Grewia tembensis green fruits	1.6	1.3	0
Hibiscus flavifolius fruits	1.1	0.7	0
H. spp. fruits	0.8	0.5	0
Lycium europaeum leaves	0.6	0.0	0
" " "	0.7	0.0	-
Sanasavieria intermedia swollen bases	0.7	0.0	-
" " fruits	1.0	1.7	-
Solanum incanum green fruits	2.5	0.0	+
" " " "	2.8	0.0	-
" " ripe fruits	3.3	0.0	++
S. spp. unripe fruits	0.9	0.0	-
Spp. leaves	0.6	0.0	0

4.ACACIAS

Acacia brevispicata leaflets	10.5	5.3	+++
" " young pods	4.8	15.2	-
A.etbaica young pods	9.1	*	0
" " "	6.7	*	-
" mature pods	7.8	*	0
" " "	8.6	*	-
" flowers (+pedicel)	5.6	2.2	-
" flowers (-pedicel)	5.2	1.9	+
" flowers (-pedicel)	6.4	1.9	-
" soft green thorns	5.6	0.0	0
A.mellifera young pods	2.0	3.4	+
" " "	1.0	1.3	+
" " "	1.5	3.1	-
" mature pods	1.2	2.5	+
" " "	1.9	3.3	-
" dry seeds	0.6	0.9	-
" " "	0.7	1.2	-

APPENDIX IIIb, cont.

A.mellifera flowers (-pedicel)	2.7	2.3	+
" dry flowers (-pedicel)	2.2	0.9	-
A.nilotica pods (-seeds)	7.2	7.6	++
" fresh seed kernels	0.5	0.7	0
" " " "	0.7	0.8	0
" fresh seed skins	8.2	14.3	0
" " " "	7.3	21.6	-
" flowers (+pedicel)	10.7	3.0	+
A.tortilis pods (-seeds)	6.4	8.5	-
" fresh seeds (+skins)	1.8	3.9	0
" flowers (+pedicel)	4.9	4.5	0
A.seyal pods (-seeds)	5.6	2.3	0
" fresh seeds (+skins)	3.6	9.8	-
" fresh seed kernels	0.4	0.0	0
" " " "	0.6	0.8	-
" fresh seed skins	7.5	12.1	0
5.OTHER TREES			
Canthium phyllanthoidium fruits	0.9	0.0	0
Commiphora coricea leaves	0.9	1.4	0
6.EUPHORBIAS			
Euphorbia nyikae fleshy stems	2.1	1.4	0
E. spp. (*heterochroma*?) stems	0.8	0.0	0
" " "	0.9	0.0	-
7.MISCELLANEOUS			
Mushrooms spp.	0.1	0.0	-
Caterpillars spp.	1.2	0.0	-

Notes: composition determined as follows; water by drying to constant weight, protein by micro-Kjeldahl method, fibre by acid-detergent method, lipids by ether extraction, phenolics by Folin-Denis method (tannic acid equivalents), tannins by modified butanol-HCL method (quebracho tannin equivalents), alkaloids according to strength of reaction to Dragendorf's reagent (see Whiten *et al.*, in press).